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By Lauren E. Hall

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Wetland Habitat and Occupancy of the Imperiled Copper-bellied Watersnake (Nerodia erythrogaster neglecta) and Other Herpetofauna

For the degree of Master of Science

Is approved by the final examining committee:

Bruce A. Kingsbury
Chair

Mark A. Jordan

Jordan M. Marshall

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Approved by Major Professor(s): Bruce A. Kingsbury

Approved by: Frank V. Paladino 12/10/2015

Head of the Departmental Graduate Program Date

WETLAND HABITAT AND OCCUPANCY OF THE IMPERILED COPPER-BELLIED WATERSNAKE (*NERODIA ERYTHROGASTER NEGLECTA*) AND OTHER HERPETOFAUNA

A Thesis

Submitted to the Faculty

of

Purdue University

by

Lauren E. Hall

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

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Fort Wayne, Indiana

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ABSTRACT

Hall, Lauren E. M.S., Purdue University, December 2015. Wetland Habitat and Occupancy of the Imperiled Copper-bellied Watersnake (*Nerodia erythrogaster neglecta*) and Other Herpetofauna. Major Professor: Bruce A. Kingsbury.

Reptile species and populations are declining globally (Gibbons *et al*., 2000). Some of the main factors leading to this decline are habitat destruction and degradation, so delineation of key habitat for reptiles for protection and restoration is particularly important for reptile conservation. Long-term efforts to monitor populations are also critical if declines are to be noticed and their causes determined. One such effort involves monitoring the Northern population segment (NPS) of Copper-bellied Watersnakes, *Nerodia erythrogaster neglecta*, which is geographically isolated from other populations and is listed as federally threatened by the US Fish and Wildlife Service. Copperbellies are also endangered in three states in which NPS occurs (MI, OH, and IN). The objective of the current study was to use occupancy modeling as part of ongoing monitoring efforts for the NPS and build upon previous studies of habitat preferences of copperbellies. I also estimated abundance and density of copperbellies at a portion of sites in the Northern population segment's range, and compared population parameter estimates for copperbellies to those of its

more common sympatric congener, the Northern Watersnake (*Nerodia sipedon sipedon*). There were very few detections of copperbellies over the course of this 2 year study, resulting in low sample sizes and difficulty in ascertaining habitat effects on occupancy of copperbellies. Abundance estimates, density estimates, and occupancy estimates for copperbellies were all low, especially compared to estimates for Northern Watersnakes. Furthermore, estimates of wetland colonization rates were very low for copperbellies, but extinction rates were high. These results are alarming, but consistent with findings of previous occupancy studies done in the area (Lee & Kingsbury, 2014). Model assumptions are discussed, and recommendations for future studies and management are given.

INTRODUCTION

Reptile species and populations are declining globally, and some of the main factors leading to this decline are habitat destruction, degradation, and fragmentation (Gibbons *et al*., 2000). Without remediation of these factors, population declines, extirpations, and even extinction of species are likely to continue. Therefore, protection and restoration of key habitat for reptiles is particularly important for their conservation. However, compared to the much-publicized and well-documented global amphibian decline, the decline in reptiles has not received as much attention. This is alarming as the declines being experienced by reptiles are often as severe as amphibian declines in magnitude, range, and taxonomic extent (Gibbons *et al*., 2000).

Documenting declines and other trends in reptile populations can be challenging for a number of reasons. Many reptile species are secretive or cryptic and therefore difficult to detect in field studies (Mazerolle *et al*., 2007). Low population densities and the rareness of high-density congregating events such as those found in breeding amphibians present other challenges in reptile surveying (Gibbons *et al*., 2000). Long-term studies of snakes are rare relative to other vertebrate groups, making declines in snake populations or distribution difficult to detect (Reading *et al.*, 2010). Lastly, even when a decline is suspected

it is difficult to determine if it can be attributed to natural population fluctuations or if it has anthropogenic causes (Gibbons *et al*., 2000). Although there are many challenges when studying reptile populations, long-term efforts to monitor populations are critical if declines are to be noticed and their causes determined.

One such effort involves monitoring populations of the imperiled Copper-bellied Watersnake, hereafter referred to as “copperbellies”. Copperbellies are a phenotypically distinct variety of the Plain-bellied Watersnake (*Nerodia erythrogaster*), formerly recognized as a subspecies, *N. e. neglecta* (Conant, 1949; Pruitt and Szymanski, 1997). A recent phylogeographic analysis using mitochondrial markers from *Nerodia erythrogaster*’s phenotypic variants suggested that there is little molecular support for distinct subspecies of Plain-bellied Watersnakes (Makowsky *et al*., 2010). Based on this finding, the standardized nomenclatural recommendation (provided in Crother (2012)) for all former subspecies is *Nerodia erythrogaster*, the Plain-bellied Watersnake. However, for the purposes of clarification within this document, I will refer to the populations formerly known as Copper-bellied Watersnakes as copperbellies while acknowledging that nomenclatural and taxonomic discussions are beyond the scope of the current study.

There are several geographically-isolated populations of copperbellies, which are separated from each other by up to 180 miles (Pruitt & Szymanski, 1997). For regulatory purposes, the United States Fish and Wildlife Service (FWS) recognizes two distinct population segments of copperbellies: the Southern population segment which encompasses all populations south of 40°N

latitude (approximately level with Indianapolis, IN) and includes disjunct populations in Illinois, Indiana, and Kentucky, and the Northern population segment which includes the few remaining populations north of this line. The Northern population segment occurs in south-central Michigan, northwestern Ohio, and northeastern Indiana. Due to the huge distance between the population segments, it is unlikely that there is any movement of individuals between them. Furthermore, habitat destruction in the area occupied by the Northern population segment has been extensive in the last two centuries, and this has led to substantial declines in the distribution and numbers of the copperbellies (Pruitt & Szymanski, 1997). Due to these circumstances, the Northern population segment of copperbellies is listed as federally threatened by the FWS under the Endangered Species Act of 1973. Copperbellies are also protected as endangered species by the three states in which the Northern population segment occurs (MI, OH, and IN).

The Northern population segment is comprised of several populations patchily distributed in suitable habitat fragments in several counties near the tri-state borders. The landscape is situated in the Upper St. Joseph River Watershed, and contains both ephemeral and permanent wetlands of various sizes and habitat types (shrub-scrub, forested, open, emergent vegetation) and an upland matrix including old fields, agricultural fields, mesic and dry-mesic southern forests, shrub-scrub, residences, and roads (Roe *et al., 2004*, Kost *et* al., 2006, Attum *et al*., 2009).

Since their federal listing in 1997, there have been many studies of copperbelly populations in the area occupied by the Northern population segment. These studies provide information about copperbelly spatial ecology (for example, Roe *et al.*, 2003, Roe *et al*., 2004), macrohabitat usage (Herbert, 2003), prey utilization (Roe *et al*., 2004), comparative ecology with sympatric congeners (Roe *et al*., 2006, Lee *et al*., 2007), metapopulation structure (Attum *et al*., 2008), abundance estimates (Lee *et al*., 2007, Attum *et al*., 2009), and occupancy rates (for example, Lee & Kingsbury, 2014), as well as summaries of habitat types in the area (Kost *et al*., 2006, Lee *et al*., 2005, Lee *et al*., 2007).

Roe *et al*. (2003) used comparative radiotelemetry to determine differences in wetland and upland use between copperbellies and a more abundant sympatric congener, the Northern Watersnake (*Nerodia sipedon sipedon*), a subspecies of the Common Watersnake (Crother, 2012). They found that copperbellies used a greater number of wetlands, used small wetlands more frequently, and used uplands during the active season more than Northern Watersnakes (hereafter “northerns”) did. Simulations showed that the loss of small ephemeral wetlands would greatly impact how copperbellies interact with the landscape but would have a minimal impact on northerns (Roe *et al.*, 2003). Roe *et al.* (2004) used comparative radiotelemetry to analyze differences in movement patterns between copperbellies and northerns, and also examined differences in diet between the two congeners. They found that copperbellies were much more vagile, moving twice as far on average and using areas up to four times as large as northerns did. Furthermore, copperbellies sometimes

moved more than 100 meters in a day and utilized almost 16 hectares per year on average. The authors also found that copperbellies preyed on anurans almost exclusively, whereas prey items for northerns were made up of approximately half fish and half anurans (Roe *et al.*, 2004). The findings of Roe *et al.* (2003) and Roe *et al*. (2004) taken together indicate that the reasons for the differences in abundance between relatively common northerns and relatively rare copperbellies may have to do with different movement patterns and landscape usage. These differences may also be brought upon by differences in prey utilization: northerns tend to be generalists and copperbellies tend to be specialists on prey whose distribution is affected by the drying of ephemeral wetlands (Roe *et al*., 2004).

Herbert (2003) used radiotelemetry and compositional analysis to investigate macrohabitat usage by copperbellies and northerns. He found that copperbellies used more macrohabitat types than northerns on average and were found at more macrohabitat types. Copperbellies also spent significant time (often more than a week) in uplands, and engaged in a large variety of behaviors in uplands. These behaviors included shedding, hibernating, sheltering from inclement weather, giving birth, digesting, and recovering from injuries. Herbert also used polytomous logistic regression to identify important microhabitat variables associated with copperbelly use. These included open canopy cover, presence of water in wetlands, proximity to shoreline or habitat margins. Additionally, copperbellies in the Northern population segment use habitats with plentiful herbaceous ground cover and shrub cover overhead, and were

frequently observed perched on logs (Herbert, 2003). Herbert further compared his findings with microhabitat preferences of copperbellies discussed by Hyslop (2001), who studied copperbellies in the Southern population segment. She found that canopy cover, log and tree cover, bare ground, and leaf litter all were associated (positively or negatively) with copperbelly use, which is a similar finding to Herbert's: copperbellies use stratified microhabitats with herbaceous vegetation and shrub cover, woody structures, and open canopy (Herbert, 2003).

Kost *et al*. (2006) delineated habitat characteristics at 9 sites in Michigan and Ohio with extant or historical copperbelly populations with the aim of characterizing community types where copperbellies occur or occurred. They looked at presence of invasive species, soil types and erosion, human alterations to wetland hydrology, vegetation structure and types, and community types of both upland and wetland areas. Their characterizations indicate that within the range of extant or historical copperbelly populations in Michigan and Ohio, there are a large variety of wetland and upland habitat types. Furthermore, the vegetation structure and types (including invasive species) at the wetlands in these areas varied substantially (Kost *et al.*, 2006).

Roe *et al*. (2006) simulated the effect of road mortality for copperbellies and northerns based on their movement patterns, and predicted copperbellies to have four times higher road mortality per year than northerns (14-21% compared to 3-5%). This study emphasized that substantial mortality for vagile wetland species can occur in terrestrial habitat between wetlands if that habitat is unsuitable.

Lee *et al.* (2005) and Lee *et al.* (2007) used various habitat modeling techniques to identify important landscape-level habitat features and construct predictive distribution maps. They identified soil type in uplands, wetland density and habitat density in 180 meter^2 blocks, wetland variety, and elevation or slope changes to be important for copperbellies. Shoreline length and wetland size were also evaluated as predictors of copperbelly activity, with shoreline length being a stronger predictor than overall wetland size. Lee *et al*. (2007) extrapolated copperbelly population size for the entire Northern population segment as 113$\pm$27 individuals, which was fewer than the raw number of observations of northerns (169 individuals) from just a portion of the study site, and noted that there were fewer copperbelly observations during this survey period compared to 2001 and 2003 in wetlands considered to be “hotspots” for copperbelly activity. They also compared population densities and detection probabilities of copperbellies and northerns. Copperbelly density was estimated at 1.09 to 2.84 snakes per hectare, compared to 6.56 to 10.41 northerns per hectare. Detection probabilities were 0.77 and 0.48 respectively for copperbellies and northerns. They also noted that 42% of copperbellies observed were on logs or downed woody debris, 19% were found in shrubs, 17% were found in herbaceous vegetation, 5% were located on grasses, and 15% were in the water. Lastly, the presence of a condition that appeared to be blister disease was also noted in several copperbellies captured during 2005 and 2006, including one instance leading to the death of a snake (Lee *et al.*, 2007)

Attum *et al*. (2008) tested how factors influencing metapopulation structure (connectivity between patches, connectivity quality, and patch size) affected distribution of rare and common species, including copperbellies and northerns respectively. They found that copperbellies were more likely to occupy wetlands farther from roads, but the distribution of common species including northerns was not influenced by proximity to roads. Forested area inside a 250 meter buffer around wetlands also was a good predictor of copperbelly occupancy. These two results indicate that although wetland patches may be "connected" by short distances, quality of the connection is a very important factor influencing distribution of rare species such as copperbellies (Attum *et al*., 2008).

Attum *et al*. (2009) used shoreline transect surveys and distance sampling to estimate the "best-case scenario" population size of the Northern population segment. They estimated total population of adult copperbellies in this area to be 94 ± 22, with population density between 0.93 to 1.87 individuals per hectare. These estimates are similar in magnitude to the estimates of Lee *et al.* (2007), above. The authors cite other studies which estimated population density in southern populations at approximately ten times this amount (10-14 snakes per hectare (Lacki *et al*., 1994) and 11 snakes per hectare (Laurent, 2000)), and recommended that the federal status of the Northern population segment be increased to endangered (Attum *et al*., 2009).

Monfils & Lee (2011), Lee *et al*. (2011), and Lee & Kingsbury (2014) investigated the use of occupancy modeling to evaluate population parameters for copperbellies, estimate population size and density of their study sites, and

start a monitoring program for northern populations of copperbellies. They used occupancy data from 2005, 2006, 2011, 2012, and 2013 from extant sites in Michigan and Ohio. Population estimates from these studies ranged from 19.7 to 69.4 individuals (these should not be compared to other estimates, as they are estimates from only a portion of total sites) and densities ranged from 0.08 to 0.48 snakes per site. Copperbelly occupancy probabilities ranged from 0.08 to 0.38 depending on which models they used, and detection probabilities were estimated between 0.19 and 0.83, with most detection probabilities lower than 0.38.

Occupancy modeling is a technique used for estimating species occupancy and other population parameters such as site colonization and extinction rates, while taking into account detection probabilities less than one (Mackenzie *et al*., 2002, Mackenzie *et al*., 2003). Detection histories are built from data of species detections and non-detections at multiple sites from repeated visits. They consist of 1s, 0s, and dashes (-), which respectively signify presence of species, non-detection of species (which may or may not equate to absence), and missing observations. Detection histories are inputted into Program PRESENCE (Hines, 2006), which can fit various models to the data. The basic parameters estimated using PRESENCE are occupancy probability (ψ) and detection probability (p) in single-season models (Mackenzie *et al*., 2002), as well as colonization (γ) and extinction (ε) probabilities between seasons in multiple-season models (Mackenzie *et al*., 2003). These parameters can be held constant or set to vary with covariates, survey, or year in different

models. Covariates can be a source of heterogeneity in parameters and can be survey-specific (such as temperature, humidity, rainfall, etc.) and affect detection probability, or site-specific (such as type of wetland, soil type, canopy cover, etc.) and affect occupancy probability, colonization probability, and extinction probability. Models are ranked using Akaike's Information Criterion (AIC). Each model is also given an Akaike weight (*w*), which is the probability of it being the best model based on the data and candidate set of models. The ratio of Akaike weights (called the evidence ratio) for two models indicates how much more likely one model is than the other (Burnham & Anderson, 2002). PRESENCE can also be used to estimate population size, using detection histories like those described above (Royle & Nichols, 2003) or count data from repeated surveys at multiple sites (Royle, 2004).

My study is intended to build on the foundation laid by Monfils & Lee (2011), Lee *et al*. (2011), and Lee & Kingsbury (2014) for a long-term monitoring program for the Northern population segment of copperbellies using occupancy modeling. I used program PRESENCE to select the best models to estimate population parameters based on two seasons of copperbelly occupancy data from 56 wetlands within their northern range. Parameters estimated include occupancy, detection probability, colonization and extinction between seasons, and population size, and I factored in the influence of habitat and survey covariates. I also compared parameters for copperbellies to parameters for their more common congener, Northern Watersnakes. The parameter estimates from

this study can be used as additional baseline data for continued monitoring of the imperiled Northern population segment of Copper-bellied Watersnakes.

METHODS

Study Site

The study site is located in the tri-state area of Michigan (Hillsdale Co.), Indiana (Steuben Co.), and Ohio (Williams Co.), where copperbellies in the northern population segment have been observed or where potentially suitable habitat occurs. The region is rural, with agricultural fields and natural areas including forest stands making up most of the landscape. The sites surveyed include land owned by Pioneer Scout Reservation and the Ohio Department of Natural Resources (Lake La Su An Wildlife Area).

Wetland complexes used in this study were previously identified for use in other studies by Bruce Kingsbury. He used GIS to place 100 meter buffers around individual wetlands. Complexes include all or most of the wetlands within 200 meters of each other that do not have roads between them. These wetlands include ephemeral wetlands, which are wet for part of the year and dry out later in the year, and permanent bodies of water. Specific complexes and wetlands were selected for surveying due to having historical (*circa* 1987 – 2001) or recent (2001 – 2006) copperbelly sightings (USFWS, 2008). A total of 63 National Wetlands Inventory (NWI) wetlands from 12 wetland complexes were initially surveyed in 2013. During 2013 and 2014, I changed the number of wetlands by

removing, adding, dividing, or combining wetlands where it made sense to do so, resulting in 56 wetlands from 12 wetland complexes included in the final analysis. The changes I made were removal of 8 wetlands because their habitat had changed significantly (either through invasive species infiltration, human activities, or becoming permanently dry), addition of 2 wetlands which had been restored for the purpose of copperbelly conservation, division of 2 NWI-delineated wetlands into 4 distinct wetlands because there was always a substantial barrier of dry land between them, and combination of 5 NWI-delineated wetlands into 2 survey wetlands because they were continuous with each other with no dry land between them.

Occupancy Data Collection

I collected occupancy data for copperbellies and northerns by shoreline surveys. Occupancy data collection was carried out following the same procedures as previous occupancy studies by Monfils & Lee (2011), Lee *et al*. (2011), and Lee & Kingsbury (2014). I used a handheld GPS to locate each wetland within the chosen complexes, and surveyed full or partial shorelines of each wetland based on the predetermined routes delineated by the USFWS. Surveying consisted of one to three observers walking around the shore of each wetland at a pace which they found comfortable, recording all visual encounters of reptiles and amphibians, and stopping occasionally to look ahead and behind the observer(s) using binoculars. The observer(s) stood in one spot and searched the upcoming and previous segments of shoreline to the extent visible

with binoculars, then continued walking until they reached the farthest point visible with binoculars from their previous vantage point, and surveyed again with binoculars. In surveys with multiple observers, we either walked together in the same direction along the same wetland, walked in opposite directions on a wetland border and met up on the other side, or each observer surveyed a different wetland at the same time. The data collected at each wetland included number of individuals sighted and GPS coordinates and time for each individual. Whenever possible, photo vouchers were taken to help confirm copperbelly sightings. I surveyed wetlands three times each in 2013, and two or three times each in 2014. The smaller amount of surveys in 2014 was due to time and personnel constraints. During each survey window, I surveyed every wetland before starting the next survey window and repeating any wetland. During 2013, the survey window dates were April 29 – May 6, May 15 – May 30, and June 7 – June 20. During 2014, the survey window dates were May 6 – May 24, May 26 – June 6, and June 13 – June 27.

Data Collection of Survey-Specific Covariates

During the occupancy surveys of 2013 and 2014, I collected covariate information that might influence detection probabilities of copperbellies at the time of each survey. These covariates included date, time of day, air temperature, wind, cloud cover, precipitation, and wetland type. All of these covariates were recorded before and after each wetland complex survey with the

exception of wetland type, which was recorded at each individual wetland as it was surveyed.

I recorded time on a 24 hour clock and I recorded temperature in Celsius. I ranked wind from 0 to 6 using the Beaufort wind scale, which uses movement of objects to estimate wind speed. I coded cloud cover from 0 to 5 (0 = 0 – 5% cover, 1 = 6 – 25%, 2 = 26 – 50%, 3 = 51 – 75%, 4 = 75 – 100%, and 5 = fog or haze). A scale of 0 to 4 was used to code precipitation. I only undertook surveys during conditions in which it might be possible to view copperbellies (Kingsbury, 2001). For example, based on surveyor discretion, surveys were not undertaken if the temperature was below 16 °C or if precipitation occurred, because snakes are not likely to be out in the open and visible under these conditions.

I classified each wetland based on visual identification using a simplified version of the wetland classification system of Cowardin *et al*. (1979) as one of the following types: palustrine forested wetland (PFW), palustrine scrub-shrub (PSS), palustrine emergent wetland (PEM SEDGE), or palustrine open water (POW). Palustrine indicates a non-flowing freshwater wetland, and each wetland is further classified based on its dominant vegetation type (PFWs have greater than 30% tree canopy cover, PSSs have greater than 30% shrub cover and less than 30% tree canopy cover, PEMs are dominated by sedges or cattails with less than 30% tree canopy cover or shrub cover). Because vegetation structure changes throughout the year, a wetland can be classified differently at different survey windows as vegetation fills in.

Data Collection of Site-Specific Covariates

Between September 6 and November 3 of 2014, I recorded habitat characteristics which might be biologically meaningful for copperbelly population parameters for all wetlands at which occupancy data were collected. These characteristics included characterization of microhabitats at the shoreline, as well as at 5, 10, 15, and 20 meter intervals from the shoreline; percentages of shrub cover, subcanopy cover, canopy cover, and emergent vegetation; emergent vegetation types; shrub identification; water depth; soil type; presence and amount of aquatic vegetation and woody debris; ephemeral or permanent status; and wetland border length. I recorded presence of buttonbush (*Cephalanthus occidentalis*) and ash trees (*Fraxinus* spp.) as well. Many previous studies have alluded to a possible preferences shared by copperbellies and buttonbush for certain latent wetland characteristics (Kingsbury & Coppola, 2000, Kingsbury, 2001, Lacki *et al*., 2005, Lee *et al*., 2011). Although ash trees have not specifically been mentioned in relation to copperbellies, I recorded their presence as well based on the same logic as recording buttonbush.

I quantified shoreline microhabitat by walking the shoreline of each wetland and recording the total amount of each type of microhabitat observed. Shoreline microhabitats were classified as one of the following: cattails, grasses, wildflowers, shrubs, woody debris, leaf litter, trees, ash trees, bare ground, mud, moss, rock, and a catch-all category “other” for anything that didn’t clearly fit into the other microhabitat categories (such as artificial structures like drains and docks). At approximately equidistant points around the shoreline, I stopped and

recorded additional information. Between 4 and 30 points were recorded at each wetland, and points were spaced between 11 and 95 meters apart from each other. Length between points and number of points were loosely proportional to wetland border length (i.e., more observation points and greater distances between points at larger wetlands). At each point, macrohabitat was classified at 5, 10, 15, and 20 meter intervals from the shoreline. These macrohabitats were classified as one of the following types: forest, shrub-scrub, field or herbaceous, current agricultural field, wetland, residential, trail or road with low traffic (foot or vehicle) including mowed trails, road with medium traffic (dirt roads with few vehicles if any per hour), and road with high traffic (paved with several cars per hour at high speeds). Wetland soil type was also classified at each point (clay, silt, sand, and pebble were the four substrates found), and depth at 0.5, 1, and 3 meters from shoreline if water was present.

I visually estimated canopy cover percentages at each wetland for shrubs, subcanopy (trees approximately 4.5 meters or shorter), and canopy of trees taller than 4.5 meters. Total canopy cover for each wetland was also visually estimated and included all three of the overlapping canopy cover types as one layer. Emergent vegetation was visually estimated for each wetland as well. All of the previous percentages were calculated as percentage of the wetland's surface covered by vegetation or canopy.

I recorded presence of ash trees and button bush within the wetland or along the shoreline, as well as types of aquatic vegetation and shrubs within or along the wetland border. Ash tree populations in the study area have been

decimated by the emerald ash borer (*Agrilus planipennis*), so all ash trees observed in the area were dead. Ash trees were identified by the distinctive feeding galleries left by larval beetles in the bark of the trees. Aquatic vegetation and woody debris in the water were both ranked on 0 to 3 scales in a semicircle with a 1 meter radius around each observation point: 0 represented absence, 1 represented an amount smaller than one-third of the semicircle, 2 represented an amount between one-third and two-thirds, and 3 represented an amount larger than two-thirds.

I classified each wetland as ephemeral or permanent based on whether water was present and the amount of water relative to the wetland's border in the spring. Wetland borders were calculated in meters using a combination of GPS and ground-truthing and were measured as the border of the wetland when it is full in springtime (the high water line) to keep procedures consistent between all wetlands regardless of how much water was present at time of measuring.

Selection of Covariates

In order to avoid data dredging (Burnham & Anderson, 2002), I made an effort to minimize the number of covariates tested during modeling. I only collected data for covariates that might be biologically meaningful in relation to population parameters of herpetofauna. I also removed strongly correlated covariates, and excluded some covariates *a priori* due to missing values, lack of variation, or observer bias. For a full list of covariates considered, see Tables 1 and 2.

Table 1. Continuous and categorical survey-specific covariates collected.

Covariate	**Type**
Temperature (°C)	Continuous
Julian day	Continuous
Sky code	Continuous
Wind code	Continuous
Precipitation code	Continuous
Survey start time	Continuous
Survey end time	Continuous
Duration	Continuous
Observer 1, 2, 3	Categorical
Wetland type	Categorical

Table 2. Continuous and categorical site-specific covariates collected.

Covariate	Type
Average aquatic vegetation taken at shoreline points	Continuous
Average woody vegetation taken at shoreline points	Continuous
Total canopy cover	Continuous
Tree canopy cover	Continuous
Subcanopy cover	Continuous
Shrub canopy cover	Continuous
Percentage emergent vegetation	Continuous
Total border length	Continuous
Shoreline cattail microhabitat	Continuous
Shoreline herbaceous microhabitat	Continuous
Shoreline shrub microhabitat	Continuous
Shoreline woody microhabitat	Continuous
Shoreline ground microhabitat	Continuous
Shoreline tree microhabitat	Continuous
Macrohabitat forest	Continuous
Macrohabitat shrub-scrub	Continuous
Macrohabitat herbaceous or field	Continuous

Table 2, continued.

Macrohabitat low traffic road	Continuous
Macrohabitat medium or high traffic road	Continuous
Water depth	Continuous
Contains water	Categorical
Presence of dead ash trees	Categorical
Presence of button bush	Categorical
Palustrine open water wetland (POW)	Categorical
Palustrine shrub-scrub wetland (PSS)	Categorical
Palustrine forested wetland (PFW)	Categorical
Palustrine emergent wetland dominated by sedges (PEM/SEDGE)	Categorical
Soil type	Categorical

I used Pearson's product-moment correlation to test for correlation between covariates. Because of the high number of correlation tests I performed for site-specific covariates, I adjusted the p-values for these comparisons to control for type I errors by implementing the Benjamini-Hochberg procedure for multiple comparisons. I used a false discovery rate of 0.001 (0.1%) to ensure removal of closely correlated covariates. To minimize the number of covariates remaining, I tallied the number of correlations to other covariates for every

covariate (Tables 3 and A1). The covariate with the highest count of other covariates correlated to it was kept, and the covariates to which it correlated were removed, then the process was repeated until no correlated covariates remained. For example, if “total canopy cover” had 12 other covariates correlated to it (Table A1), each of those 12 covariates was removed prior to model formation, but if occupancy probability varied by “total canopy cover”, inferences could potentially be made about the other 12 covariates based on correlation with this covariate.

Data Formatting

I formatted the 2013 and 2014 occupancy data for copperbellies and northerns into detection histories for use in occupancy analyses.

Covariates that might influence detection probabilities were put into charts so that there was one value for each wetland for each survey occasion. Survey date was converted to Julian day and temperatures were averaged to give a single value per survey per wetland. Julian day and average temperature were converted to z-scores for 2013 and 2014 for single-season models, and combined z-scores for multiple-season models. Pre- and post-survey wind, sky, and precipitation codes were also averaged to obtain a single value per survey per wetland, and were converted to z-scores for 2013, 2014, and combined 2013 and 2014 data. Categorical wetland types (e.g., POW, PSS) were coded as dummy variables using 1s and 0s.

Site-specific covariates were formatted into dummy variables if they were categorical, and into z-scores if they were continuous.

Model Construction and Selection

I constructed all models using Program PRESENCE 9.9. Models were constructed with parameters either constant (indicated in model names as "(.)"), varying with site- or survey-specific covariates, or with p differing between years, surveys (1-1, 1-2, 1-3, 2-1, 2-2, 2-3), or windows (the same window in different years would have the same detection probability in this case). I used AIC_c to rank models instead of AIC due to small sample size, and used the number of wetland sites (55 in 2013 and 56 in 2014 and multi-season analyses) as the effective sample size (Mackenzie *et al*., 2006). Furthermore, I tested goodness-of-fit for single-season models using ĉ values provided in model outputs. I used ĉ as a variance inflation factor in instances of overdispersion (when ĉ of the top-ranked model was greater than one, based on 1000 bootstraps) and changed the model selection criterion to $QAIC_c$ (Mackenzie & Bailey, 2004). For multi-season models, no robust goodness-of-fit tests are currently available, so I followed the approach of Cooch & White (2006): I incrementally increased ĉ in the results browser from 1 to 2 to qualitatively examine which models were the top-ranked and if these rankings changed for different ĉ values. If a model output indicated it did not reach numerical convergence, I ran it again after supplying initial values of beta parameters from the simplest model ($\psi(.)p(.)$ for single-season models, $\psi(.)p(.)\gamma(.)\varepsilon(.)$ for multiple-season models). In cases where numerical

convergence (to a minimum of 3 significant digits) was not reached even after supplying reasonable initial values or in cases where models converged but beta parameters had unreasonably large values, these models were excluded *a posteriori* and I indicated it in the Results section.

I considered a model to have reasonable support if ΔAIC_c was 0-2. Values of ΔAIC_c greater than 10 have no support (Burnham & Anderson, 2002). I also used Akaike weights (*w*) to compare top-ranked models. The ratio of two models' Akaike weights indicates how likely one model is compared to the other (Burnham & Anderson, 2002). I used beta parameter estimates from outputs of supported models to assess directional effects of site- and survey-specific covariates on population parameters. I used the model averaging feature in PRESENCE to retrieve estimates of population parameters averaged over the whole candidate set of models, taking into account model weight. I attempted to present results based on the suggestions for information-theoretic analyses of Anderson *et al.* (2001).

Single-Season Models

I determined which models to construct for single-season analyses based on the following process: 1) run all models with constant ψ first to test effects of survey-specific covariates on detection probability and note which models have the most support (ΔAIC_c or $\Delta qAIC_c$ less than two), 2) run models with constant p to test effects of site-specific covariates on ψ and note which models have the most support (ΔAIC_c or $\Delta qAIC_c$ less than two), 3) run models with combinations

of covariates from the most-supported models (both survey- and site-specific). So for example, if ψ(.)p(temp) was the most supported model in the first step and ψ(CANOPY),p(.) was the most supported model in the second step, in the third step I also ran the model ψ(CANOPY),p(temp). In the absence of numerical convergence issues, if there were multiple supported models with site-specific covariates influencing ψ I ran combinations of those models as well.

I used the same candidate set of models for both copperbellies and northerns in order to compare population parameters and covariate effects for the two species where applicable.

Multiple-Season Models

With 10 site-specific covariates and 4 survey-specific covariates, the number of possible multiple-season models is over 6,000. In order to keep the candidate set of models manageable and minimize overparameterization of models, I only analyzed models for one population parameter at a time. In other words, I held three of the four population parameters (ψ, γ, ε, and p) constant and varied the fourth with covariates. A fifth parameter, λ, is derived in the PRESENCE model output using the equation $\lambda_t = \frac{\psi_{t+1}}{\psi_t}$ (Mackenzie *et al*., 2003). This parameter represents rate of change in occupancy between years. Values less than 1 represent a decrease in occupancy from the first year to the second and values greater than 1 represent an increase in occupancy.

As with single-season models, I used the same candidate set of models for both copperbellies and northerns in order to compare population parameters and covariate effects for the two species where applicable.

Royle N-Mixture Models

I used Royle N-Mixture models to estimate population size for the sites I surveyed. This model is also called the Repeated Count Data model or Royle Biometrics model in PRESENCE. Detection histories constructed of number of individuals observed (instead of 1s and 0s) are used in these models. These models estimate two parameters, abundance per site (λ for Poisson spatial distribution and μ for negative binomial distribution) and detection probability (r), with two additional parameters derived, occupancy estimate ($\psi_{derived}$) and total abundance (*a*). I compared models with a Poisson distribution (the default model in PRESENCE) or a negative binomial distribution (which seems a more realistic distribution because habitat is not homogeneous in the area and snakes are not likely to be randomly distributed at wetland sites) for the prior spatial distribution. I also executed these models for northerns to make comparisons of population parameters with copperbelly population parameters.

These models consistently gave low estimates of detection probability compared to model-averaged estimates from single-season candidate model sets. I considered it unlikely that detection probability is constant for either species throughout the whole season. Therefore, I also substituted detection

probability values from model averaging of single-season models and ran the Royle N-Mixture models again.

RESULTS

Covariate Selection

Due to correlations with other covariates, survey-specific covariates duration and observer were removed. Duration was found to be correlated to site-specific covariate wetland border (r = 0.781), so the duration covariate was excluded. Because observer 1 and 2 were correlated covariates, all observers were excluded because determining effects of observer on detection probability is not meaningful without considering all primary observers (Table 3).

Site-specific covariates that were correlated (Table A1) were also removed. The removed covariates were ephemeral or permanent; average woody abundance at shoreline points; presence of dead ash; tree, subcanopy, and shrub canopy cover; POW, PSS, and PFW; shoreline percentage of herbaceous cover, tree cover, and ground cover; and macrohabitat forest and medium-to-high traffic road cover types.

Some covariates were also excluded *a priori*. The excluded covariates were soil type, depth, precipitation code, and wetland start and end times. Although soil type was considered biologically meaningful (heavy-textured soils inhibit water drainage, allowing wetland formation, and copperbellies hibernate in crayfish burrows constructed in clay soils; Lee *et al*., 2007, Kost *et al*., 2006), I

excluded soil type because there was very little variation in types observed – almost all wetlands had only clay as the substrate. Depth was excluded because at the time habitat covariates were recorded, many wetlands were dry. When using site-specific covariates in occupancy modeling in PRESENCE, there can be no missing values. It is likely that depth at high water line is correlated to other covariates I used, such as ephemeral or permanent, and total wetland border, so inferences about depth might still be made based on inclusion of these covariates. Precipitation code was excluded because surveys were only undertaken when there was no precipitation in order to increase chances of seeing snakes. Wetland start and end times were also excluded because they all fell within the acceptable range based on Kingsbury's (2001) protocol, and the start times were not independently distributed due to logistical constraints in 2013, and observer constraints between 2013 and 2014. Anecdotally, at the wetlands where copperbellies are most consistently observed, I have seen copperbellies in the very early morning near sunrise up until sunset, in the heat of mid-afternoon, and on chilly early mornings. While time of day may influence likelihood of copperbelly (or northern) observation, the biases in survey start times in the present study prevented their use as a covariate in these analyses.

After testing for correlation, three more site-specific covariates were removed: PEM/SEDGE because there were very few wetlands of this type (n=5, less than 10% of the total wetlands), average aquatic vegetation taken at points around the wetland because it was a very similar measure to another included covariate (total emergent vegetation), and roads with medium or high traffic,

because most wetlands had a value of zero for this covariate and the wetlands that had nonzero values almost always had roads with low traffic nearby as well.

After removal of correlated covariates and *a priori* exclusion of covariates, 14 total covariates remained, 4 of which were survey-specific and 10 of which were site-specific. Table 4 provides a list of the 14 covariates and their abbreviated names used in modeling.

Table 3. Pearson's product-moment correlation values (r) for survey-specific covariates. Bold values highlight correlated covariates. Number of correlations for each covariate includes correlations from rows and columns with the covariate name.

	temp	**day**	**sky**	**wind**	**observer 1**	**observer 2**
day	-0.099					
sky	-0.212	-0.245				
wind	0.094	-0.381	0.124			
observer 1	-0.170	0.063	-0.089	-0.043		
observer 2	0.242	-0.159	-0.039	-0.006	**-0.725**	
observer 3	-0.043	0.291	0.121	-0.176	-0.048	-0.081
# of Correlations	*0*	*0*	*0*	*0*	*1*	*1*

Table 4. Final list of covariates included in candidate model sets. Abbreviations and type of covariate (site- or survey-specific) are listed.

Covariate Description	Abbreviation	Type of Covariate
Temperature (°C)	temp	Survey
Julian day	day	Survey
Sky code	sky	Survey
Wind code	wind	Survey
Presence of buttonbush	BUTTON	Site
Percentage total canopy cover	CANOPY	Site
Percentage emergent vegetation cover	EMERGENT	Site
Total wetland border length	BORDER	Site
Percentage of shoreline cattail cover	SHORECATTAIL	Site
Percentage of shoreline shrub cover	SHORESHRUB	Site
Percentage of shoreline woody debris cover	SHOREWOOD	Site
Percentage of macrohabitat shrub-scrub	MACROSHRUB	Site
Percentage of macrohabitat herbaceous cover or field	MACROHERB	Site
Percentage of macrohabitat roads with low or foot traffic	ROADLOW	Site

2013 Single-Season Models for Copperbellies and Northerns

In 2013, there were 7 copperbelly detections (12 individual snakes observed). Twelve complexes comprising 55 wetlands were surveyed for a total of 163 surveys. The naïve occupancy rate was 0.0909. During the first survey

period there were 4 detections and in the second survey period there were 3 detections. There were no detections during the third survey period in 2013. Single-season models and rankings for copperbellies for 2013 are shown in Tables 5 and 6. Two models (ψ(.),p(wind) and ψ(SHORESHRUB),p(.)) failed to reach numerical convergence and were removed from the candidate set. Model averaging produced parameter estimates of ψ = 0.1019, p_1 = 0.8137, p_2 = 0.4349, and p_3= 0.0457, which are displayed in Table 26 for comparison to other model-averaged estimates.

In 2013, there were 28 northern detections (51 individual snakes observed) out of 163 surveys. The naïve occupancy rate was 0.4000. During the first survey period there were 13 detections, in the second survey period there were 8 detections, and in the third survey period there were 7 detections. The number of individuals observed in the first, second, and third survey periods were 27, 16, and 8 respectively. Single-season models and rankings for northerns for 2013 are shown in Tables 7 – 9. One model, ψ(BORDER),p(.), failed to converge and was removed from the final candidate model set. The null model was kept for model averaging for parameter estimates, but was removed from the final candidate set (Table 9) because it was originally listed as the top model. Model averaging produced parameter estimates of ψ = 0.7453, p_1 = 0.2439, p_2 = 0.2278, and p_3= 0.2180, which are displayed in Table 27 for comparison to other model-averaged estimates.

2014 Single-Season Models for Copperbellies and Northerns

In 2014, there were 7 copperbelly detections (14 individual snakes observed). Twelve complexes comprising 56 wetlands were surveyed for a total of 136 surveys (eight complexes were only surveyed twice, the remaining four complexes were surveyed three times). The naïve occupancy rate was 0.0714. During the first survey period there were 3 detections, during the second survey period there were 2 detections, and during the third survey period there were 2 detections. Single-season models and rankings for copperbellies for 2014 are shown in Tables 10 and 11. All 2014 models in the copperbelly candidate set reached numerical convergence. Model averaging produced parameter estimates of ψ = 0.0808, p_1 = 0.6554, p_2 = 0.5262, and p_3= 0.5990, and are displayed in Table 26 for comparison to other model averaged estimates.

In 2014, there were 28 northern detections (48 individual snakes observed) out of 136 surveys. The naïve occupancy rate was 0.3393. During the first survey period there were 14 detections, during the second survey period there were 10 detections, and during the third survey period there were 4 detections. These corresponded to 23, 14, and 11 individual observations respectively. Single-season models and rankings for northerns for 2014 are shown in Tables 12 and 13. All 2014 models in the northern candidate set reached numerical convergence. Model averaging produced parameter estimates of ψ = 0.4262, p_1 = 0.5492, p_2 = 0.4380, and p_3= 0.4404, and are displayed in Table 27 for comparison to other model averaged estimates

Table 5. Survey-specific covariates affecting detection probability, 2013 single-season Copper-bellied Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
ψ(.),p(day)	49.55	0.00	0.5513	3
ψ(.),p(survey)	50.41	0.86	0.3586	3
ψ(.),p(temp)	53.98	4.43	0.0602	3
ψ(.),p(.)	56.00	6.45	0.0219	2
ψ(.),p(sky)	58.02	8.47	0.0080	3

Table 6. Final model set including survey- and site-specific covariates, 2013 single-season Copper-bellied Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
ψ(BORDER),p(day)	41.19	0.00	0.8219	4
ψ(BORDER),p(survey)	44.82	3.63	0.1338	5
ψ(BORDER),p(.)	48.45	7.26	0.0218	3
ψ(.),p(day)	49.55	8.36	0.0126	3
ψ(SHOREWOOD),p(.)	52.14	10.95	0.0034	3
ψ(.),p(survey)	52.74	11.55	0.0026	4
ψ(.),p(temp)	53.98	12.79	0.0014	3
ψ(.),p(.)	56.00	14.81	0.0005	2
ψ(ROADLOW),p(.)	56.26	15.07	0.0004	3
ψ(EMERGENT),p(.)	56.56	15.37	0.0004	3
ψ(BUTTON),p(.)	56.74	15.55	0.0003	3
ψ(CANOPY),p(.)	57.85	16.66	0.0002	3
ψ(MACROSHRUB),p(.)	57.91	16.72	0.0002	3
ψ(.),p(SKY)	58.02	16.83	0.0002	3
ψ(MACROHERB),p(.)	58.22	17.03	0.0002	3
ψ(SHORECATTAIL),p(.)	58.24	17.05	0.0002	3

Table 7. Survey-specific covariates affecting detection probability, 2013 single-season Northern Watersnake models.

Model	QAICc	ΔQAICc	*w*	*k*
ψ(.),p(.)	137.76	0.00	0.2961	2
ψ(.),p(day)	138.10	0.34	0.2498	3
ψ(.),p(temp)	139.36	1.60	0.1330	3
ψ(.),p(sky)	139.68	1.92	0.1134	3
ψ(.),p(survey)	139.72	1.96	0.1111	4
ψ(.),p(wind)	140.00	2.24	0.0966	3

Table 8. Candidate model set including survey- and site-specific covariates, 2013 single-season Northern Watersnake models.

Model	QAICc	ΔQAICc	*w*	*k*
ψ(.),p(.)	137.76	0.00	0.1552	2
ψ(.),p(day)	138.10	0.34	0.1309	3
ψ(BUTTON),p(.)	139.05	1.29	0.0814	3
ψ(.),p(temp)	139.36	1.60	0.0697	3
ψ(SHORECATTAIL),p(.)	139.61	1.85	0.0615	3
ψ(SHORESHRUB),p(.)	139.63	1.87	0.0609	3
ψ(.),p(sky)	139.68	1.92	0.0594	3
ψ(SHOREWOOD),p(.)	139.71	1.95	0.0585	3
ψ(.),p(survey)	139.72	1.96	0.0583	4
ψ(EMERGENT),p(.)	139.83	2.07	0.0551	3
ψ(CANOPY),p(.)	139.88	2.12	0.0538	3
ψ(MACROSHRUB),p(.)	139.88	2.12	0.0538	3
ψ(ROADLOW),p(.)	140.00	2.24	0.0506	3
ψ(MACROHERB),p(.)	140.00	2.24	0.0506	3

Table 9. Final model set including survey- and site-specific covariates, 2013 single-season Northern Watersnake models. The null model has been removed.

Model	AICc	ΔAICc	*w*	*k*
ψ(.),p(day)	153.09	0.00	0.1655	3
ψ(BUTTON),p(.)	154.15	1.06	0.0974	3
ψ(.),p(temp)	154.49	1.4	0.0822	3
ψ(.),p(survey)	154.63	1.54	0.0766	4
ψ(SHORECATTAIL),p(.)	154.77	1.68	0.0714	3
ψ(SHORESHRUB),p(.)	154.80	1.71	0.0704	3
ψ(.),p(sky)	154.85	1.76	0.0686	3
ψ(SHOREWOOD),p(.)	154.88	1.79	0.0676	3
ψ(EMERGENT),p(.)	155.02	1.93	0.0630	3
ψ(MACROSHRUB),p(.)	155.07	1.98	0.0615	3
ψ(CANOPY),p(.)	155.08	1.99	0.0612	3
ψ(MACROHERB),p(.)	155.21	2.12	0.0573	3
ψ(ROADLOW),p(.)	155.21	2.12	0.0573	3

Table 10. Survey-specific covariates affecting detection probability, 2014 single-season Copper-bellied Watersnake models.

Model	QAICc	ΔQAICc	*w*	*k*
ψ(.),p(.)	27.79	0.00	0.3673	2
ψ(.),p(temp)	28.76	0.97	0.2262	3
ψ(.),p(day)	29.98	2.19	0.1229	3
ψ(.),p(sky)	30.03	2.24	0.1199	3
ψ(.),p(wind)	30.03	2.24	0.1199	3
ψ(.),p(survey)	32.04	4.25	0.0439	4

Table 11. Final model set including survey- and site-specific covariates, 2014 single-season Copper-bellied Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
ψ(BORDER+SHOREWOOD),p(temp)	39.14	0.00	0.3215	5
ψ(BORDER+SHOREWOOD),p(.)	39.30	0.16	0.2968	4
ψ(BORDER),p(temp)	41.29	2.15	0.1097	4
ψ(BORDER),p(.)	41.32	2.18	0.1081	3
ψ(SHOREWOOD),p(temp)	42.65	3.51	0.0556	4
ψ(SHOREWOOD),p(.)	42.87	3.73	0.0498	3
ψ(.),p(temp)	46.37	7.23	0.0087	3
ψ(.),p(.)	46.41	7.27	0.0085	2
ψ(SHORESHRUB),p(.)	46.46	7.32	0.0083	3
ψ(ROADLOW),p(.)	47.25	8.11	0.0056	3
ψ(MACROSHRUB),p(.)	48.40	9.26	0.0031	3
ψ(CANOPY),p(.)	48.47	9.33	0.0030	3
ψ(EMERGENT),p(.)	48.47	9.33	0.0030	3
ψ(MACROHERB),p(.)	48.47	9.33	0.0030	3
ψ(.),p(day)	48.55	9.41	0.0029	3
ψ(BUTTON),p(.)	48.61	9.47	0.0028	3
ψ(.),p(wind)	48.64	9.50	0.0028	3
ψ(SHORECATTAIL),p(.)	48.64	9.50	0.0028	3
ψ(.),p(sky)	48.64	9.50	0.0028	3
ψ(.),p(survey)	50.41	11.27	0.0011	4

Table 12. Survey-specific covariates affecting detection probability, 2014 single-season Northern Watersnake models.

Model	QAICc	ΔQAICc	*w*	*k*
ψ(.),p(temp)	104.19	0.00	0.3277	3
ψ(.),p(day)	105.00	0.81	0.2186	3
ψ(.),p(.)	105.04	0.85	0.2142	2
ψ(.),p(sky)	106.50	2.31	0.1032	3
ψ(.),p(wind)	106.92	2.73	0.0837	3
ψ(.),p(survey)	107.85	3.66	0.0526	4

Table 13. Final model set including survey- and site-specific covariates, 2014 single-season Northern Watersnake models.

Model	QAICc	ΔQAICc	*w*	*k*
ψ(BORDER),p(temp)	101.49	0.00	0.4284	4
ψ(BORDER),p(day)	102.43	0.94	0.2677	4
ψ (BORDER),p(.)	102.84	1.35	0.2181	3
ψ(SHORESHRUB),p(.)	104.94	3.45	0.0763	3
ψ(.),p(temp)	112.26	10.77	0.002	3
ψ(SHORECATTAIL),p(.)	113.03	11.54	0.0013	3
ψ(.),p(day)	113.14	11.65	0.0013	3
ψ(.),p(.)	113.36	11.87	0.0011	2
ψ(MACROSHRUB),p(.)	114.13	12.64	0.0008	3
ψ(ROADLOW),p(.)	114.25	12.76	0.0007	3
ψ(CANOPY),p(.)	114.68	13.19	0.0006	3
ψ(SHOREWOOD),p(.)	115.01	13.52	0.0005	3
ψ(BUTTON),p(.)	115.46	13.97	0.0004	3
ψ(MACROHERB),p(.)	115.55	14.06	0.0004	3
ψ(EMERGENT),p(.)	115.59	14.10	0.0004	3

Multiple-Season Models for Copperbellies and Northerns

There were a total of 14 copperbelly detections (26 individual observations) over the two survey years (2013 and 2014). The naïve occupancy rate was 0.125. Twelve complexes comprising 56 wetlands were surveyed for a total of 299 surveys. All but three wetlands were surveyed 5 or 6 times. Two wetlands were surveyed 4 times and one wetland was surveyed just once. At the 7 wetlands at which I detected copperbellies, the number of detections throughout the study ranged from 1 to 4. Rate of detection at these wetlands

ranged from 0.167 to 0.667, with a mean of 0.338. There were 49 wetlands at which no detections of copperbellies were confirmed.

Copperbelly multiple-season models and their rankings are shown in Tables 14 through 20. All models with covariates affecting copperbelly detection probability (p) reached numerical convergence (Table 14). When ĉ for this model set was changed from 1 to 2, the order of model rankings switched (Tables 14 and 15). In the candidate model set for covariates affecting copperbelly occupancy probability (ψ) the only model that failed to reach numerical convergence, ψ(SHORESHRUB), γ(.),ε(.),p(.), was removed (Table 16). In the candidate model set for covariates affecting copperbelly colonization probability (γ), ψ(.),γ(SHORECATTAIL),ε(.),p(.) did not reach numerical convergence and thus was removed (Table 17). Table 18 shows the final candidate set for covariates affecting colonization probability with the null model removed. For models affecting copperbelly extinction probability (ε), models including BORDER, CANOPY, SHORECATTAIL, SHORESHRUB, and EMERGENT all failed to converge, and were therefore removed (Table 19). Table 20 shows the final candidate set for covariates affecting extinction probability with the null model removed.

Model averaging produced parameter estimates for copperbellies for each candidate set of models which are displayed in Table 26 for comparison to other model averaged estimates.

There were a total of 56 detections of northerns (99 individual observations) over the two survey years. The naïve occupancy rate was 0.5357. I

detected northerns at 30 of the 56 wetlands surveyed. There number of detections per wetland ranged from 1 to 6 throughout the study. Rate of detection at these wetlands ranged from 0.167 to 1. There were 26 wetlands with no detections of northerns confirmed.

Northern multiple-season models and their rankings are shown in Tables 21 – 25. All models with covariates affecting northern detection probability (p) converged (Table 21). When ĉ for this model set was changed from 1 to 2, the order of model rankings switched (Tables 21 and 22). For models with covariates affecting northern occupancy probability (ψ), those including SHOREWOOD, EMERGENT, and CANOPY failed to converge and were therefore removed (Table 23). In the candidate model set for covariates affecting northern colonization probability (γ), ψ(.),γ(SHORECATTAIL),ε(.),p(.) did not reach numerical convergence and thus was removed (Table 24). For models affecting northern extinction probability (ε), the models with MACROSHRUB and SHOREWOOD both failed to converge, and were therefore removed (Table 25).

Model averaging produced parameter estimates for northerns for each candidate set of models which are displayed in Table 27 for comparison to other model averaged estimates.

Table 14. Survey-specific covariates affecting detection probability, multi-season Copper-bellied Watersnake models, ĉ = 1.

Model	AICc	ΔAICc	*w*	*k*
$\psi(.),\gamma(.),\varepsilon(.),p$(wind)	94.74	0.00	0.5853	5
$\psi(.),\gamma(.),\varepsilon(.),p$(day)	96.90	2.16	0.1988	5
$\psi(.),\gamma(.),\varepsilon(.),p(.)$	98.85	4.11	0.0750	4
$\psi(.),\gamma(.),\varepsilon(.),p$(window)	99.72	4.98	0.0485	6
$\psi(.),\gamma(.),\varepsilon(.),p$(year)	100.29	5.55	0.0365	5
$\psi(.),\gamma(.),\varepsilon(.),p$(temp)	101.26	6.52	0.0225	5
$\psi(.),\gamma(.),\varepsilon(.),p$(sky)	101.27	6.53	0.0224	5
$\psi(.),\gamma(.),\varepsilon(.),p$(survey)	102.66	7.92	0.0112	9

Table 15. Survey-specific covariates affecting detection probability, multi-season Copper-bellied Watersnake models, ĉ = 2.

Model	QAICc	ΔQAICc	*w*	*k*
$\psi(.),\gamma(.),\varepsilon(.),p$(wind)	52.97	0.00	0.3289	5
$\psi(.),\gamma(.),\varepsilon(.),p(.)$	53.82	0.85	0.2150	4
$\psi(.),\gamma(.),\varepsilon(.),p$(day)	54.05	1.08	0.1917	5
$\psi(.),\gamma(.),\varepsilon(.),p$(year)	55.75	2.78	0.0819	5
$\psi(.),\gamma(.),\varepsilon(.),p$(temp)	56.23	3.26	0.0644	5
$\psi(.),\gamma(.),\varepsilon(.),p$(sky)	56.23	3.26	0.0644	5
$\psi(.),\gamma(.),\varepsilon(.),p$(window)	56.72	3.75	0.0504	6
$\psi(.),\gamma(.),\varepsilon(.),p$(survey)	62.29	9.32	0.0031	9

Table 16. Site-specific covariates affecting occupancy probability, multi-season Copper-bellied Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
ψ(BORDER),γ(.),ε(.),p(.)	91.16	0.00	0.7653	5
ψ(SHOREWOOD),γ(.),ε(.),p(.)	94.22	3.06	0.1657	5
ψ(.),γ(.),ε(.),p(.)	98.85	7.69	0.0164	4
ψ(ROADLOW),γ(.),ε(.),p(.)	99.54	8.38	0.0116	5
ψ(BUTTON),γ(.),ε(.),p(.)	99.76	8.60	0.0104	5
ψ(EMERGENT),γ(.),ε(.),p(.)	99.88	8.72	0.0098	5
ψ(CANOPY),γ(.),ε(.),p(.)	101.02	9.86	0.0055	5
ψ(MACROSHRUB),γ(.),ε(.),p(.)	101.04	9.88	0.0055	5
ψ(MACROHERB),γ(.),ε(.),p(.)	101.25	10.09	0.0049	5
ψ(SHORECATTAIL),γ(.),ε(.),p(.)	101.26	10.10	0.0049	5

Table 17. Site-specific covariates affecting colonization probability, multi-season Copper-bellied Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
ψ(.),γ(.),ε(.),p(.)	98.85	0.00	0.2116	4
ψ(.),γ(SHOREWOOD),ε(.),p(.)	99.18	0.33	0.1794	5
ψ(.),γ(CANOPY),ε(.),p(.)	100.43	1.58	0.0960	5
ψ(.),γ(EMERGENT),ε(.),p(.)	100.62	1.77	0.0873	5
ψ(.),γ(SHORESHRUB),ε(.),p(.)	100.73	1.88	0.0826	5
ψ(.),γ(MACROSHRUB),ε(.),p(.)	100.86	2.01	0.0774	5
ψ(.),γ(ROADLOW),ε(.),p(.)	100.92	2.07	0.0751	5
ψ(.),γ(BORDER),ε(.),p(.)	101.24	2.39	0.0640	5
ψ(.),γ(MACROHERB),ε(.),p(.)	101.26	2.41	0.0634	5
ψ(.),γ(BUTTON),ε(.),p(.)	101.27	2.42	0.0631	5

Table 18. Site-specific covariates affecting colonization probability, multi-season Copper-bellied Watersnake models with null model removed.

Model	AICc	ΔAICc	*w*	*k*
$\psi(.),\gamma$(SHOREWOOD),$\varepsilon(.),p(.)$	99.18	0.00	0.2275	5
$\psi(.),\gamma$(CANOPY),$\varepsilon(.),p(.)$	100.43	1.25	0.1218	5
$\psi(.),\gamma$(EMERGENT),$\varepsilon(.),p(.)$	100.62	1.44	0.1107	5
$\psi(.),\gamma$(SHORESHRUB),$\varepsilon(.),p(.)$	100.73	1.55	0.1048	5
$\psi(.),\gamma$(MACROSHRUB),$\varepsilon(.),p(.)$	100.86	1.68	0.0982	5
$\psi(.),\gamma$(ROADLOW),$\varepsilon(.),p(.)$	100.92	1.74	0.0953	5
$\psi(.),\gamma$(BORDER),$\varepsilon(.),p(.)$	101.24	2.06	0.0812	5
$\psi(.),\gamma$(MACROHERB),$\varepsilon(.),p(.)$	101.26	2.08	0.0804	5
$\psi(.),\gamma$(BUTTON),$\varepsilon(.),p(.)$	101.27	2.09	0.08	5

Table 19. Site-specific covariates affecting extinction probability, multi-season Copper-bellied Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
$\psi(.),\gamma(.),\varepsilon(.),p(.)$	98.85	0.00	0.2401	4
$\psi(.),\gamma(.),\varepsilon$(ROADLOW),$p(.)$	99.37	0.52	0.1852	5
$\psi(.),\gamma(.),\varepsilon$(BUTTON),$p(.)$	99.51	0.66	0.1726	5
$\psi(.),\gamma(.),\varepsilon$(SHOREWOOD),$p(.)$	100.25	1.40	0.1193	5
$\psi(.),\gamma(.),\varepsilon$(MACROSHRUB),$p(.)$	100.29	1.44	0.1169	5
$\psi(.),\gamma(.),\varepsilon$(MACROHERB),$p(.)$	100.72	1.87	0.0943	5

Table 20. Site-specific covariates affecting extinction probability, multi-season Copper-bellied Watersnake models with null model removed.

Model	AICc	ΔAICc	*w*	*k*
$\psi(.),\gamma(.),\varepsilon$(ROADLOW),$p(.)$	99.37	0.00	0.269	5
$\psi(.),\gamma(.),\varepsilon$(BUTTON),$p(.)$	99.51	0.14	0.2509	5
$\psi(.),\gamma(.),\varepsilon$(SHOREWOOD),$p(.)$	100.25	0.88	0.1733	5
$\psi(.),\gamma(.),\varepsilon$(MACROSHRUB),$p(.)$	100.29	0.92	0.1698	5
$\psi(.),\gamma(.),\varepsilon$(MACROHERB),$p(.)$	100.72	1.35	0.137	5

Table 21. Survey-specific covariates affecting detection probability, multi-season Northern Watersnake models, ĉ = 1.

Model	AICc	ΔAICc	*w*	*k*
ψ(.),γ(.),ε(.), p(temp)	281.9	0	0.3443	5
ψ(.),γ(.),ε(.), p(day)	282.77	0.87	0.2228	5
ψ(.),γ(.),ε(.), p(year)	283.28	1.38	0.1727	5
ψ(.),γ(.),ε(.), p(.)	283.78	1.88	0.1345	4
ψ(.),γ(.),ε(.), p(sky)	284.93	3.03	0.0757	5
ψ(.),γ(.),ε(.), p(wind)	286.1	4.2	0.0422	5
ψ(.),γ(.),ε(.), p(survey)	289.46	7.56	0.0079	9

Table 22. Survey-specific covariates affecting detection probability, multi-season Northern Watersnake models, ĉ = 2.

Model	QAICc	ΔQAICc	*w*	*k*
ψ(.),γ(.),ε(.),p(.)	146.28	0	0.2549	4
ψ(.),γ(.),ε(.),p(temp)	146.55	0.27	0.2227	5
ψ(.),γ(.),ε(.),p(day)	146.98	0.7	0.1796	5
ψ(.),γ(.),ε(.),p(year)	147.24	0.96	0.1577	5
ψ(.),γ(.),ε(.),p(sky)	148.06	1.78	0.1047	5
ψ(.),γ(.),ε(.),p(wind)	148.65	2.37	0.0779	5
ψ(.),γ(.),ε(.),p(survey)	155.69	9.41	0.0023	9

Table 23. Site-specific covariates affecting occupancy probability, multi-season Northern Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
ψ(BORDER),γ(.),ε(.),p(.)	276.65	0.00	0.9253	5
ψ(SHORESHRUB),γ(.),ε(.),p(.)	282.28	5.63	0.0554	5
ψ(.),γ(.),ε(.),p(.)	286.48	9.83	0.0068	4
ψ(BUTTON),γ(.),ε(.),p(.)	287.82	11.17	0.0035	5
ψ(MACROSHRUB),γ(.),ε(.),p(.)	288.35	11.7	0.0027	5
ψ(ROADLOW),γ(.),ε(.),p(.)	288.67	12.02	0.0023	5
ψ(SHORECATTAIL),γ(.),ε(.),p(.)	288.86	12.21	0.0021	5
ψ(MACROHERB),γ(.),ε(.),p(.)	288.90	12.25	0.002	5

Table 24. Site-specific covariates affecting colonization probability, multi-season Northern Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
ψ(.),γ(SHORESHRUB),ε(.),p(.)	276.13	0.00	0.7652	5
ψ(.),γ(BORDER),ε(.),p(.)	279.11	2.98	0.1725	5
ψ(.),γ(.),ε(.),p(.)	283.78	7.65	0.0167	4
ψ(.),γ(CANOPY),ε(.),p(.)	284.72	8.59	0.0104	5
ψ(.),γ(SHOREWOOD),ε(.),p(.)	285.64	9.51	0.0066	5
ψ(.),γ(ROADLOW),ε(.),p(.)	285.65	9.52	0.0066	5
ψ(.),γ(MACROSHRUB),ε(.),p(.)	285.72	9.59	0.0063	5
ψ(.),γ(BUTTON),ε(.),p(.)	285.96	9.83	0.0056	5
ψ(.),γ(EMERGENT),ε(.),p(.)	286.14	10.01	0.0051	5
ψ(.),γ(MACROHERB),ε(.),p(.)	286.19	10.06	0.005	5

Table 25. Site-specific covariates affecting extinction probability, multi-season Northern Watersnake models.

Model	AICc	ΔAICc	*w*	*k*
$\psi(.),\gamma(.),\varepsilon$(BORDER),$p$(.)	276.94	0	0.6272	5
$\psi(.),\gamma(.),\varepsilon$(SHORESHRUB),$p$(.)	278.33	1.39	0.313	5
$\psi(.),\gamma(.),\varepsilon(.),p$(.)	283.78	6.84	0.0205	4
$\psi(.),\gamma(.),\varepsilon$(ROADLOW),$p$(.)	284.86	7.92	0.012	5
$\psi(.),\gamma(.),\varepsilon$(SHORECATTAIL),$p$(.)	285.61	8.67	0.0082	5
$\psi(.),\gamma(.),\varepsilon$(MACROHERB),$p$(.)	286.01	9.07	0.0067	5
$\psi(.),\gamma(.),\varepsilon$(EMERGENT),$p$(.)	286.17	9.23	0.0062	5
$\psi(.),\gamma(.),\varepsilon$(BUTTON),$p$(.)	286.2	9.26	0.0061	5

Table 26. Model-averaged parameter estimates for Copper-bellied Watersnake candidate model sets. Single-season (SS) and multiple-season (MS) candidate model sets are shown. Bolded values indicate parameter estimates that the candidate set specifically modeled.

	2013 candidate set, SS	**2014 candidate set, SS**	**ψ candidate set, MS**	**γ candidate set, MS**	**ε candidate set, MS**	***p* candidate set, ĉ=1, MS**	***p* candidate set, ĉ =2, MS**
ψ	**0.1019**	**-**	**0.1090**	0.1104	0.1109	0.1038	0.1075
Derived ψ (2014)	-	**0.0808**	0.0922	0.0941	0.0899	0.0838	0.0871
P 1-1	**0.8137**	-	0.4439	0.4348	0.4366	**0.6462**	**0.5728**
P 1-2	**0.4349**	-	0.4439	0.4348	0.4366	**0.6097**	**0.5325**
P 1-3	**0.0457**	-	0.4439	0.4348	0.4366	**0.3253**	**0.3463**
P 2-1	-	**0.6554**	0.4439	0.4348	0.4366	**0.5791**	**0.5404**
P 2-2	-	**0.5262**	0.4439	0.4348	0.4366	**0.5951**	**0.5296**
P 2-3	-	**0.5990**	0.4439	0.4348	0.4366	**0.4554**	**0.4310**
γ	-	-	0.0435	**0.0464**	0.0450	0.0385	0.0400
ε	-	-	0.5144	0.5214	**0.5489**	0.5242	0.5211
Derived λ	-	-	1.6319	0.8532	0.8129	0.8088	0.8145

Table 27. Model-averaged parameter estimates for Northern Watersnake candidate model sets. Single-season (SS) candidate model sets are shown. Bolded values indicate parameter estimates that the candidate set specifically modeled.

	2013 candidate set, SS	**2014 candidate set, SS**	**ψ candidate set, MS**	**γ candidate set, MS**	**ε candidate set, MS**	***p* candidate set, ĉ=1, MS**	***p* candidate set, ĉ =2, MS**
ψ	**0.7453**	**-**	**0.6790**	0.5196	0.6450	0.5988	0.5977
Derived ψ (2014)	-	0.4262	0.5961	-	0.5746	-	-
P 1-1	**0.2439**	-	0.2917	0.3582	0.3140	**0.3330**	**0.3273**
P 1-2	**0.2278**	-	0.2917	0.3582	0.3140	**0.2999**	**0.3055**
P 1-3	**0.2180**	-	0.3927	0.3582	0.3140	**0.2935**	**0.2991**
P 2-1	-	0.5492	0.3927	0.3582	0.3140	**0.3947**	**0.3792**
P 2-2	-	0.4380	0.3927	0.3582	0.3140	**0.3382**	**0.3375**
P 2-3	-	0.4404	0.3927	0.3582	0.3140	**0.2198**	**0.2373**
γ	-	-	0.0042	**0.3842**	0.1942	0.1823	0.1874
ε	-	-	0.1254	0.2988	**0.3395**	0.2638	0.2543
Derived λ	-	-	1.6319	-	0.8878	-	-

Royle N-Mixture Model for Copperbellies and Northerns

Of the 4 models I ran for both copperbellies and northerns (Poisson and negative binomial with constant detection probabilities or fixed detection probabilities), one model failed to converge for both 2013 and 2014 for both species (the fixed negative binomial model, μ(.),*a*(.),*r*(.)), so it was removed from the candidate set. The rankings for the other 3 models are shown in Tables 28 – 31. Based on the top-ranked models, estimated number of individuals per site in 2013 and 2014 were 0.2061 (95% CI: 0.0674 – 0.6301) and 0.2006 (95% CI: 0.0522 – 0.7546) respectively for copperbellies and 1.4218 (95% CI: 0.9483 –

2.4421) and 0.7906 (95% CI: 0.4869 – 1.2837) respectively for northerns (Table 32). Abundance estimates for the whole study area using the top ranked models for 2013 and 2014 were 11.54 (95%CI: 3.77 – 35.29) and 11.23 (95% CI: 2.99 – 42.26) respectively for copperbellies, and were 85.22 (95%CI: 53.11 – 136.76) and 44.27 (95% CI: 27.27 – 71.89) respectively for northerns.

Table 28. Rankings for Royle N-Mixture candidate set of models for copperbellies for 2013.

Model	**AICc**	**ΔAICc**	***w***	***k***
μ(.),*a*(.),*r*(fixed)	429.50	0.00	0.9935	3
λ(.),*r*(.)	439.79	10.29	0.0058	2
λ(.),*r*(fixed)	444.00	14.50	0.0007	2

Table 29. Rankings for Royle N-Mixture candidate set of models for copperbellies for 2014.

Model	**AICc**	**ΔAICc**	***w***	***k***
μ(.),*a*(.),*r*(fixed)	425.35	0.00	0.9994	3
λ(.),*r*(.)	440.46	15.11	0.0005	2
λ(.),*r*(fixed)	445.17	19.82	0.0000	2

Table 30. Rankings for Royle N-Mixture candidate set of models for northerns for 2013.

Model	**AICc**	**ΔAICc**	***w***	***k***
μ(.),*a*(.),*r*(fixed)	582.21	0.00	1.0000	3
λ(.),*r*(fixed)	603.41	21.20	0.0000	2
λ(.),*r*(.)	604.60	22.39	0.0000	2

Table 31. Rankings for Royle N-Mixture candidate set of models for northerns for 2014.

Model	AICc	ΔAICc	*w*	*k*
μ(.),*a*(.),*r*(fixed)	549.47	0.00	0.9788	3
λ(.),*r*(fixed)	558.50	9.03	0.0107	2
λ(.),*r*(.)	558.54	9.07	0.0105	2

Table 32. Royle N-mixture model comparisons for copperbellies and northerns by year. The top-ranked models were used for these parameter estimates. Parameters displayed in this table include (constant) abundance per site (μ), detection probability (*r*) fixed to model-averaged estimates from single-season models, total abundance estimates (*a*), derived occupancy (ψ) estimates, and naïve occupancy (ψ) rates. 95% confidence intervals are shown in parentheses. Copperbellies are abbreviated CWS and northerns are abbreviated NWS. Bolded values indicate parameter estimates that the candidate set specifically modeled.

	CWS 2013	CWS 2014	NWS 2013	NWS 2014
$\boldsymbol{\mu}$	**0.2061** (0.0674 – 0.6301)	**0.2006** (0.0533 – 0.7546)	**1.5218** (0.9483 – 2.4421)	**0.7906** (0.4869 – 1.2837)
$\boldsymbol{r_1}$**(fixed)**	0.8137	0.6554	0.2439	0.5492
$\boldsymbol{r_2}$**(fixed)**	0.4349	0.5262	0.2278	0.4380
$\boldsymbol{r_3}$ **(fixed)**	0.0457	0.5990	0.2180	0.4404
$\boldsymbol{a}$	**11.54** (3.77 – 35.29)	**11.23** (2.99 – 42.26)	**85.22** (53.11 – 136.76)	**44.27** (27.27 – 71.89)
$\boldsymbol{\psi_{derived}}$	**0.0973** (0.0160 – 0.1785)	**0.0774** (0.0043 – 0.1505)	**0.5091** (0.3523 – 0.6658)	**0.3909** (0.2507 – 0.5312)
$\boldsymbol{\psi_{naïve}}$	0.0909	0.0714	0.4000	0.3393

DISCUSSION

2013 Single-Season Models for Copperbellies and Northerns

From 2013 single-season models, possible relationships between occupancy and wetland border length and between detection probability and Julian day were found. These models had some goodness-of-fit and sample size issues (see below), but the general trend for both species was that occupancy increased with wetland border length and detection decreased with increasing Julian day.

For 2013 copperbelly single-season analyses, the most supported model (ΔAIC_c less than 2) was ψ(BORDER),p(day), with a model weight of 0.8219 (see Table 6). The evidence ratio between the weights of this model and the second-ranked model is 6.14 – given the observed data and the candidate model set, the top model is 6.14 times more likely than the second-ranked model to be the best model. However, the ĉ value for the top-ranked model was 0.5232, which is indicative of underdispersion (Mackenzie & Bailey, 2004). This means that there is less variation in the observed dataset than is predicted by the model. Given the small sample size and relatively low number of detections in 2013 (especially with no detections in the third survey period), this is not surprising – with few detections it is unlikely that relationships between covariates and population

parameters can be determined with any accuracy. It should also be noted that although this model was the one with the highest AIC_c values and *w*, Akaike's information criterion and its variants are used to select the best models to describe the data from a *candidate set* presented, which may not necessarily include a model that fits the data very well. This is why it is important to carefully select which models are included in the candidate set based on possible biological meaningfulness – even if all models in the candidate set are poor predictors of actual processes, AIC still selects a "best model" relative to the quality of the other candidate models.

The beta estimates from the top-ranked copperbelly model in 2013 suggest that occupancy increases with wetland border size and detection decreases as Julian day increases. The covariates BORDER and day were not significantly correlated with any other covariate, so no inferences about other measured covariates can be made. These relationships suggested by the beta estimates of the top model (a positive relationship between border length and occupancy and a negative relationship between detection probability and day) describe trends visually apparent in the 2013 data, but this may be a coincidence, and it would be inappropriate to extrapolate information from this model to make inferences about processes influencing copperbelly population parameters on a larger scale due to small sample size and lack of fit. However the positive relationship suggested between copperbelly occupancy and wetland border length may be supported by Roe *et al*.'s (2004) study of copperbelly prey. They found that copperbellies eat a specialized diet of almost exclusively

anurans, whose distribution is affected by seasonal drying of wetlands. As smaller wetlands dry out as the summer season progresses, prey availability for copperbellies will become limited to more permanent wetlands (which tend to have longer shorelines, r = 0.4457). Roe *et al.* (2003) pointed out that copperbellies have to follow their food source as wetlands dry up because they are specialists, whereas the dietary generalist Northern Watersnake may simply shift to another food source such as fish.

As for the negative relationship suggested by the model beta parameters between Julian day and copperbelly detection probability, based on my occupancy data it is much harder to detect herpetofauna around wetlands in this area later in the season than at the beginning. A decrease in detection probability as Julian day increase is likely due to increased vegetation or reduced activity levels later in the season. As the season progresses (and Julian day increases), emergent vegetation, shoreline herbaceous vegetation, and shrubs leaf out, providing a lot more cover for copperbellies and other herpetofauna to hide in. Additionally, copperbellies become active during spring when mating season occurs, then have reduced activity during the day as air and water temperatures increase (Roe *et al*., 2004, USFWS, 2008). Roe *et al*. (2003) also found that copperbellies shifted between wetlands less frequently as summer progressed. Reduced activity levels as the season progresses will reduce detection probability as a moving snake is easier to detect than a stationary snake.

For 2013 single-season models for northerns, the top-ranked model was the null model (Table 8). The ĉ value for this model was 1.0853, which indicates

that this model does a decent job of describing the variation in the data. The parameter estimates for the null model were ψ = 0.7466 and p = 0.2297. Despite the apparent goodness-of-fit of the null model, it is unlikely that no covariates affect occupancy and detection probabilities. It may have been the best model to describe the data while not being biologically significant, so I removed it to determine if there were any effects of covariates (Table 9). Once the null model was removed, the top-ranked model was ψ(.),p(day), with a ĉ value of 0.9523. The ĉ value by itself indicates this model also does an adequate job of describing the variation in the data. However, of the 13 models in the candidate set for 2013 northern single-season models, 11 of them had a ΔAIC less than 2, and the other two models were close. Furthermore, the AIC weights for these models were all close in range (0.0573 – 0.1655). In instances where there is not a single or a few clearly superior model(s), multimodel inference using model averaging can be used to obtain parameter estimates (Burnham & Anderson, 2002). The model-averaged estimates for this candidate set were ψ = 0.7453, p_1 = 0.2439, p_2 = 0.2278, and p_3 = 0.2180 (Table 27). These estimates are actually very similar to those obtained from the null model (ψ = 0.7466 and p = 0.2297), which was removed. Because all the models were closely ranked, no covariate relationships could be discerned from the 2013 single-season model set for northerns.

The top-ranked copperbelly model for 2013 single-season models (ψ(BORDER),p(day)) gave parameter estimate ranges of ψ = 0.0192 – 0.9965, p_1 = 0.7975 – 0.8977, p_2 = 0.1836 – 0.5842, and p_3 = 0.0223 – 0.0917. Although there was a very wide range of estimates for occupancy probability, 85% of ψ

estimates were under 0.15 and the values that appeared to be outliers occurred at the wetlands with the largest border sizes, which the model predicts. The detection probability parameter estimates showed a decreasing trend as the season progressed. I compared the copperbelly parameter estimates with the model-averaged parameter estimates of northerns from 2013 single-season models (ψ = 0.7453, p_1 = 0.2439, p_2 = 0.2278, and p_3 = 0.2180). First, based on these estimates, northerns appear to have 5 or more times higher occupancy than copperbellies except at a small proportion of sites where copperbellies were predicted to occur disproportionately to their normal occupancy rates. Much higher occupancy of northerns is supported by previous studies such as Lee *et al*. (2007), who estimated copperbelly density at 1.09 to 2.84 snakes per hectare, compared to 6.56 to 10.41 northerns per hectare, and Lee & Kingsbury (2014), who observed northerns at 3 – 5 times more wetlands than copperbellies. Second, based on these estimates, detection probability appears to be relatively consistent throughout the season for northerns, compared to detection probability of copperbellies which ranges from very high to very low (0.8977 to 0.0223) from the beginning of the survey season to the end. One possible explanation for the consistent p for northerns but the varying p for copperbellies is that dietary differences between the two species vary greatly and may impact movement patterns (Roe *et al*., 2003, Roe *et al.*, 2004). Northerns have more stationary tendencies than copperbellies, possibly due to being dietary generalists. If one food source becomes limited, they may be more likely to switch to another food source than seek food at other locations. Changes in detection probability for

copperbellies may be influenced by reduced prey availability as ephemeral wetlands dry up as the season progresses (Roe *et al*., 2004). It is possible detection probability becomes so low because the copperbellies leave most sites and therefore cannot be detected at all.

2014 Single-Season Models for Copperbellies and Northerns

Similar to the findings of 2013 models, 2014 single-season models suggested that occupancy of both copperbellies and northerns has a positive relationship with wetland border length. Additionally, copperbelly occupancy was negatively correlated with percentage of shoreline woody debris, and temperature had a negative relationship with copperbelly detection probability. These models suffered the same sample size issues as those from 2013, but their goodness-of-fit to the data was better than the goodness-of-fit for 2013 models.

For 2014 single-season analyses, the most supported models for copperbellies were ψ(BORDER+SHOREWOOD),p(temp) and ψ(BORDER+SHOREWOOD),p(.) (see Table 11). The Akaike weights for the two models were 0.3215 and 0.2968 respectively. The evidence ratio (1.08) was close to 1, indicating that neither model is supported much more substantially than the other. However, the two models are very similar so similar inferences can be drawn from both models. The top-ranked model had a ĉ of 0.9966, indicating the model adequately describes the variation in the data. Similar to 2013, there was a small sample size and relatively few detections in 2014, so

although these models do a fairly good job of describing the data set available, caution should be taken to avoid making hasty generalizations about copperbelly habitat preferences as a whole.

Beta parameters for both top-ranked copperbelly models indicated that length of wetland border was positively correlated with occupancy, which was the same result found in the 2013 single-season top-ranked model. Beta parameters for these two models also suggest that percentage of the shoreline consisting of woody debris was negatively correlated with occupancy. The first model's beta parameters also indicated that detection probability was negatively correlated with temperature. These statements make sense based on the 2014 copperbelly data. The negative correlation between occupancy and percentage of shoreline consisting of woody debris in 2014 is supported by Herbert's (2003) findings that copperbellies prefer habitat with plentiful herbaceous and shrubby cover. Percentage of shoreline consisting of woody debris is negatively correlated with other shoreline cover types (r = -0.404 for herbaceous cover and r = -0.470 for shrub cover); intuitively as percentage of shoreline consisting of woody debris increases, percentage of other (possibly more preferred) cover types decreases. Lastly, a negative correlation between detection probability and air temperature as suggested by the p(temp) model makes biological sense. As temperature increases, snakes are less likely to bask out in the open to thermoregulate, meaning they will be harder to detect (Roe *et al*., 2003). However, increase in temperature may not be the only reason that detection probability decreases as the survey season progressed.

As discussed above, progression of the survey season is also correlated with increased vegetative cover and decreased copperbelly activity once the mating season is over. Although the p(temp) model may be more biologically realistic than a model with constant detection (p(.)), model-averaged estimates (Table 26) from all candidate sets with non-constant detection were relatively consistent for 2014 detection probabilities regardless of survey window, and especially when compared to the large range of detection probabilities estimated for 2013 (Table 26). Estimates of detection all ranged from 0.4310 to 0.6554 from model-averaging, which was similar to the estimate of detection probability predicted by the top-ranked model with constant detection (p = 0.5843). These estimates can be compared to estimates ranging from 0.1109 to 0.9174 for the p(temp) model. Because both models had approximately equal weights, I cannot definitively say which model is better for estimating detection probabilities, but as mentioned above, both models indicated relationships between border length and occupancy as well as shoreline percentage of woody debris and occupancy.

For 2014 single-season northern models (Table 13), the three models supported by $\Delta QAIC_c$s less than 2 all had ψ varying with BORDER, while p varied by temp, varied by day, or was constant. The combined weight of these three models is 0.9142, and the top-ranked model has a ĉ value of 0.9966, indicating goodness-of-fit. Therefore, the covariate BORDER was adequate for describing variation in occupancy for northerns in 2014. Beta parameters from these models suggest that the length of the wetland border has a positive relationship with occupancy. This result is supported by the finding of Attum *et al*.

(2008) that northerns were significantly more likely to occur in wetlands with larger border lengths. They also found that copperbellies were more likely to occur in wetlands with larger border lengths (Attum *et al*., 2008). Both of these results were supported by occupancy modeling in my study. As Attum *et al*. (2008) suggested, increased border length is likely preferred by both snake species because they primarily forage along the wetland border.

Lastly, because the three top-ranked models for northerns in 2014 had detection probability affected by three conflicting factors (detection cannot be both constant and affected by covariates), I used model-averaging to acquire population parameter estimates from this model set (Table 27). Parameters for northerns were estimated at ψ = 0.4262, p_1 = 0.5492, p_2 = 0.4380, and p_3 = 0.4404. Interestingly, occupancy appeared to decrease between years, but detection probability nearly doubled. The data do not support occupancy decreasing substantially from 2013 to 2014 (northerns were detected at 13, 8, and 7 sites in 2013 and 14, 10, and 4 sites in 2014), although naïve occupancy did decrease slightly between years (0.4000 to 0.3393). I believe the increase in detection probability really occurred, although not due to any changes in behavior of northerns. Rather, my abilities to detect herpetofauna likely increased with experience. This trend may also be supported by changes in detection probability estimates between years for copperbellies from highly variable as the season progressed in 2013 to relatively consistent throughout the season in 2014 (Table 26).

Multiple-Season Models for Copperbellies and Northerns

Multi-season models for both copperbellies and northerns again indicated a positive relationship between occupancy and wetland border length. No further covariate relationships could be ascertained from copperbelly models due to goodness-of-fit and model selection issues (see below), but model averaging provided estimates of local colonization (very low) and local extinction rates (high) for copperbellies. Northerns had colonization and extinction rates that were relatively close to each other. Models for northerns showed negative relationships between extinction probability and both wetland border length and shoreline shrub cover. Additionally, shoreline shrub cover was included in the top-ranked model for northern colonization probabilities as having a positive relationship with colonization, but this result was not significant.

For multiple-season analyses for both species, I devised candidate sets based on one population parameter varying with covariates and the other three parameters being held constant.

For the model set investigating effects of covariates on copperbelly detection probability, changing the ĉ value from 1 to 2 altered the order of the model rankings (Tables 14 and 15). This suggests that the data are too sparse for fitting complex models of detection probability such as those with covariates in the candidate data set. Because of the equivocal nature of the detection probability candidate set, not best model or models could be distinguished. Therefore, I used model-averaging for the two sets to acquire parameter estimates (Table 26). The two sets estimated similar occupancy probabilities for

both years (0.1038 and 0.1075 for 2013, 0.0838 and 0.0871 for 2014). The estimates for detection probability were also very similar to each other (see Table 26). Detection probability estimates for copperbellies ranged from 0.3253 to 0.6462

For models investigating effects of covariates on copperbelly occupancy (Table 16), the only supported model based on ΔAIC_c was ψ(BORDER),γ(.),ε(.),p(.) with an Akaike weight of 0.7653. The next best model had a ΔAIC above the threshold of 2, and the evidence ratio of the Akaike weights of the two models indicated the top-ranked model is 4.62 times more likely to be the best model as the next model. As with the single-season models, beta parameters of the top-ranked indicated a positive correlation between occupancy and wetland border length.

The null model, ψ(.),γ(.),ε(.),p(.), was the top-ranked model for copperbellies for both the γ and ε model sets, which tested the effects of covariates on site colonization and extinction probabilities respectively (Tables 17 and 19). This model was kept for the purposes of model averaging, but I removed it for further analysis of the two model sets because biologically it is unlikely that colonization and extinction probabilities are constant for all wetlands. Realistically, habitat features likely impact which wetlands get colonized or go locally extinct. Once the null models were removed (Tables 18 and 20), all models in both the colonization and extinction sets had ΔAICs less than 2 and model weights which were not substantially different from the weight of any other model. Unfortunately, because there were no clearly supported or superior

models in either set, no covariate relationships with colonization or extinction probability could be elucidated. I again utilized model-averaging to acquire parameter estimates for these model sets (Table 26).

The model-averaged estimates of copperbelly colonization and extinction probabilities were similar for both the colonization and extinction model sets (γ = 0.0464 or 0.0450, ε = 0.5214 or 0.5489). These estimates are alarming – given a much higher site extinction rate than site colonization rate, proportion of sites occupied (occupancy) will decrease over time. Furthermore, metapopulation dynamics dictate that metapopulations with extinction-prone patches when the patch network is small are more in danger of extirpation than metapopulations with large networks which are well-connected and less prone to local extinctions (Hanski, 1998).

The Northern Watersnake multi-season p candidate model sets are shown in Tables 21 and 22. As with these model sets for copperbellies, changing the ĉ value from 1 to 2 altered the order of the model rankings, indicating that no solid inferences can be made about covariate effects on detection probability based on these models. Model-averaged estimates of detection probabilities are showen in Table 27. These ranged from 0.2198 to 0.3947 for these two models.

The multi-season occupancy candidate model set for northerns (Table 23) indicated that the only supported model from this set was ψ(BORDER),γ(.),ε(.),p(.), based on ΔAIC less than 2 and *w* of 0.9253. Beta parameters from this model again indicated a positive relationship between northern occupancy and border length, which was discussed in depth in the

previous section. Again, wetland border length was positively associated with occupancy for both northerns and copperbellies. Estimates of ψ for wetlands from this model ranged from very low (0.02278) to very high (0.9952) depending on the length of the wetland border.

The only supported model from the northern colonization model set was $\psi(.),\gamma(\text{SHORESHRUB}),\varepsilon(.),p(.)$ based on ΔAIC less than 2 and a model weight of 0.7652 (Table 24). Beta parameters for this model indicated a slight positive relationship between colonization and percentage of shoreline shrub cover. However, the confidence interval for the beta parameter overlapped zero, indicating the result is not statistically significant and therefore broader inferences based on this possible relationship should not be made. No other colonization models for northerns were supported, so covariate relationships remain elusive in this case. The model-averaged estimate of colonization probability from this model set was γ = 0.3842.

From the northern multi-season extinction model set (Table 25), two models were supported based on ΔAIC, although their weights were not substantially different enough from each other (0.6272 and 0.313). These models had ε varying with BORDER and SHORESHRUB. The beta parameters from these two models indicated that extinction was negatively correlated with border and amount of shoreline shrub cover. The relationship with wetland border length makes sense given that almost all models relating to occupancy of northerns and covariates have indicated a positive relationship with border length. Intuitively then, the smaller the border length the more likely it is that northerns will not find

the habitat suitable and will leave. Furthermore, these models indicate that as shrub cover on the shoreline increases, local extinction probability decreases. This is likely because with increased cover, risk of predation should decrease. Lastly, although the extinction candidate model set for copperbellies did not yield significant results, I believe with a larger sample size, similar results would have been found for copperbellies (border length having a negative relationship with extinction probability). The model-averaged estimate of ε for the extinction probability set of models for northerns was 0.3395, which is very close to the estimate of colonization (γ = 0.3842).

Local Colonizations and Extinctions by Copperbellies

In 2014, two wetlands with no previous detections had detections (possible local colonizations), one of which was at a complex with no previous detections. Three wetlands with detections in 2013 had no detections in 2014, and one complex that had 2 detections in 2013 had no detections in 2014 (possible local extinctions). It is worth noting that the only individual I observed at the (possibly) newly-colonized wetland complex was the only juvenile copperbelly observed throughout the whole study, and was possibly a neonate (it was around 12 inches in length). The complex is located within a triangle formed with three other complexes as vertices. These complexes are the ones that had copperbelly adults observed in 2013 and are all within 600 meters of the location where the juvenile was found (a reasonable distance for adult copperbellies to travel, Roe *et al*., 2004). Neonate copperbellies appear to hibernate at the site at which they

were born (USFWS, 2008), and if this is the case for the individual I observed, a gravid adult copperbelly may have moved into the area from another complex. Minimum convex polygon (MCP) images from Roe *et al*. (2004) indicate that copperbellies in 2001 and 2002 did travel between two wetlands sites at which an adult copperbelly was detected in 2013 and the neonate was detected in 2014. The observation of a neonate copperbelly at a site with no previous detections in this study could be an example of a rescue effect between patches of a metapopulation, or there could be adult copperbellies present at this site that went undetected in my study.

Model-Averaged Parameter Estimates for Copperbellies

Model averaging was used make multimodel inferences about copperbelly population parameters from both single and multiple seasons. Values of ψ were low regardless of models used, while detection probability ranged from very low to very high values and appeared to be influenced by factors related progression of the season. Lastly, estimates of colonization probabilities were low regardless of model used, and estimates of extinction probabilities were high. Parameter estimates for different models are shown side-by-side in Figures 1 through 5. Model-averaged estimates for copperbellies are shown in Table 26, with northern parameter estimates for reference (Table 27).

Estimates of occupancy were very low for copperbellies regardless of model set used for both 2013 and 2014. Values of ψ ranged from 0.1019 to 0.1109 for 2013, and 0.0808 to 0.0922 for 2014 (see Figure 1). These estimates

are just slightly higher than naïve occupancy from 2013 and 2014 (ψ = 0.0909 and 0.0714 respectively). This could indicate that when copperbellies are present, they are almost always detected (high detection probabilities). However, model-averaged detection probability estimates (Figures 3 and 4) did not support this. Unfortunately, occupancy estimates close to naïve occupancy rates may simply indicate that there were not enough data to accurately model occupancy in this study. All 2013 estimates were slightly higher than 2014 estimates of occupancy. Furthermore, most estimates of the derived parameter lambda (rate of change in occupancy between years) were less than 1, and estimates of wetland colonization probabilities were very low (0.0385 – 0.0464) while wetland extinction probabilities were much higher (0.5144 – 0.5489) (Figure 5). All these results taken together could indicate that copperbellies used fewer sites in 2014 than 2013 (see discussion below about ψ when the closure assumption is violated). These results are also similar to those discussed by Lee & Kingsbury (2014), who reported colonization probabilities of 0.01 to 0.03 between 2011 and 2013, and extinction probabilities of 0.26 to 0.48.

For both 2013 and 2014, most estimates of detection probability for copperbellies decreased from the first survey window to the third (Figures 3 and 4). Estimates of p ranged from 0.0457 to 0.8137. As discussed above, decreases in p as the season progresses is likely caused by a combination of factors including increase in ambient temperatures throughout the season, vegetation leafing out, and possibly increased canopy cover as the season progresses making copperbellies seek more open wetlands. Although logistic constraints

prevented it in this study, I would suggest surveying more rapidly at the beginning of the year in the future, or using alternate methods for surveying to increase chances of detecting copperbellies (see discussion below of a possible alternate method).

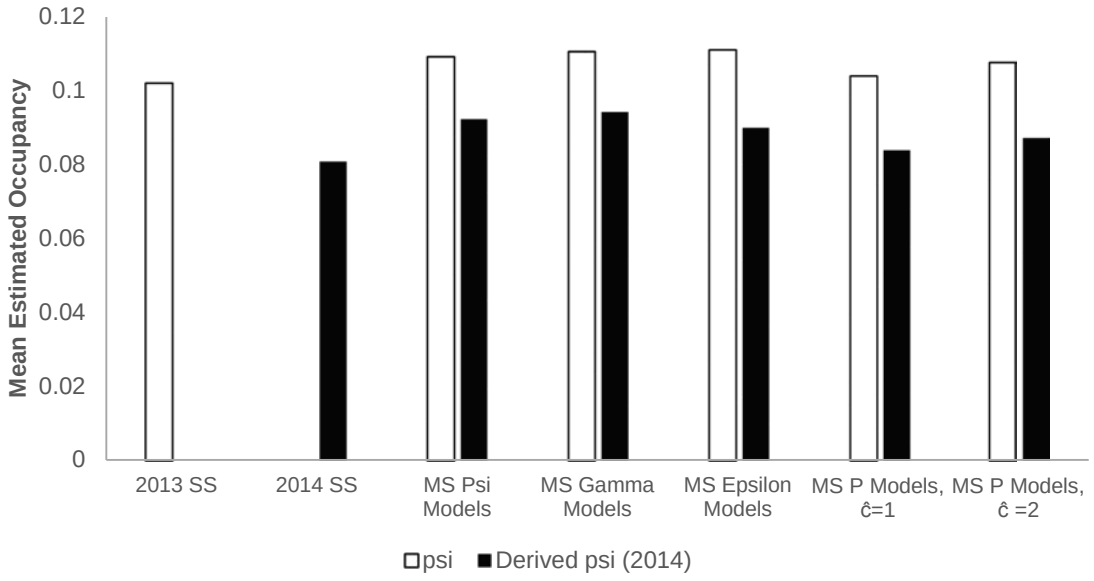

Figure 1. Model-averaged estimates of copperbelly occupancy for 2013 and 2014 from single-season and multiple-season models.

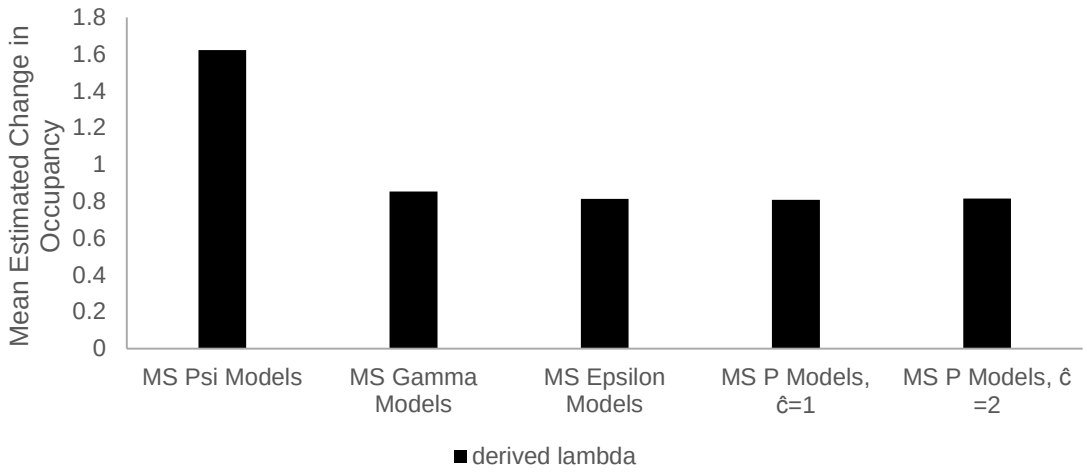

Figure 2. Model-averaged estimates of copperbelly change of occupancy between 2013 and 2014.

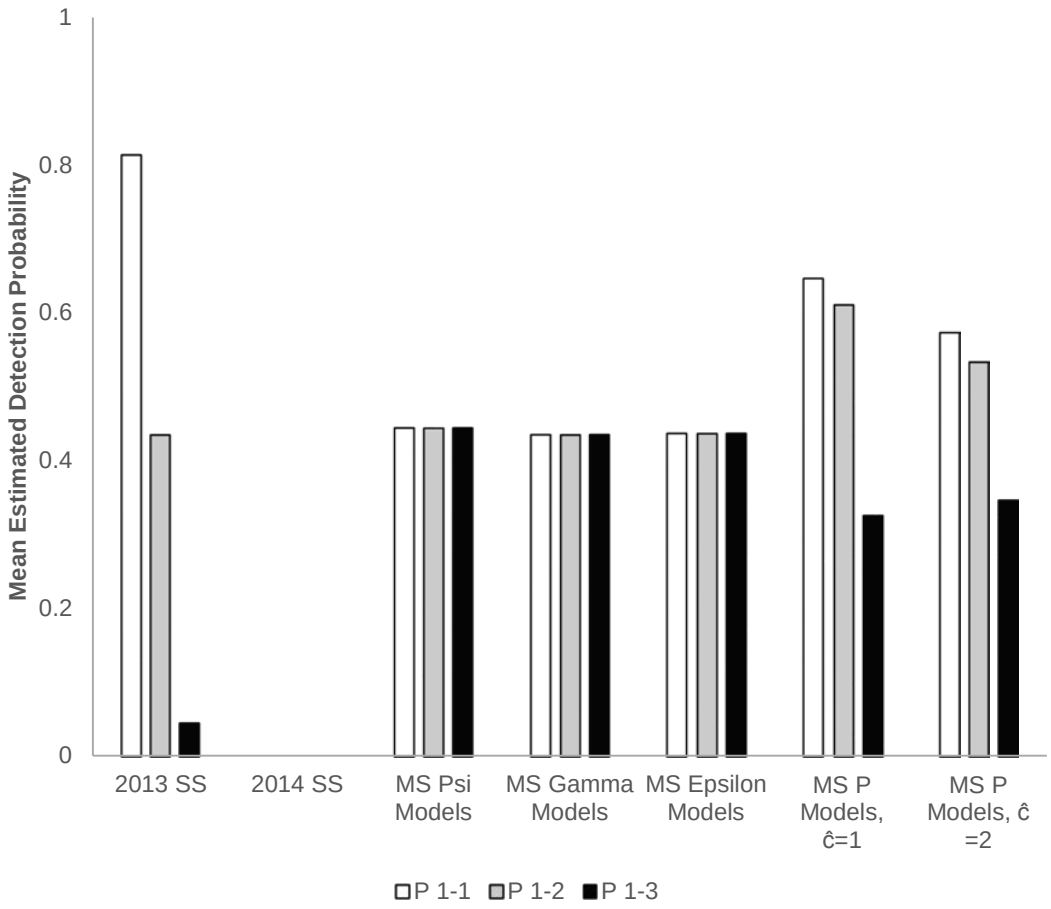

Figure 3. Model-averaged estimates of copperbelly detection probability for 2013 from single-season and multiple-season models.

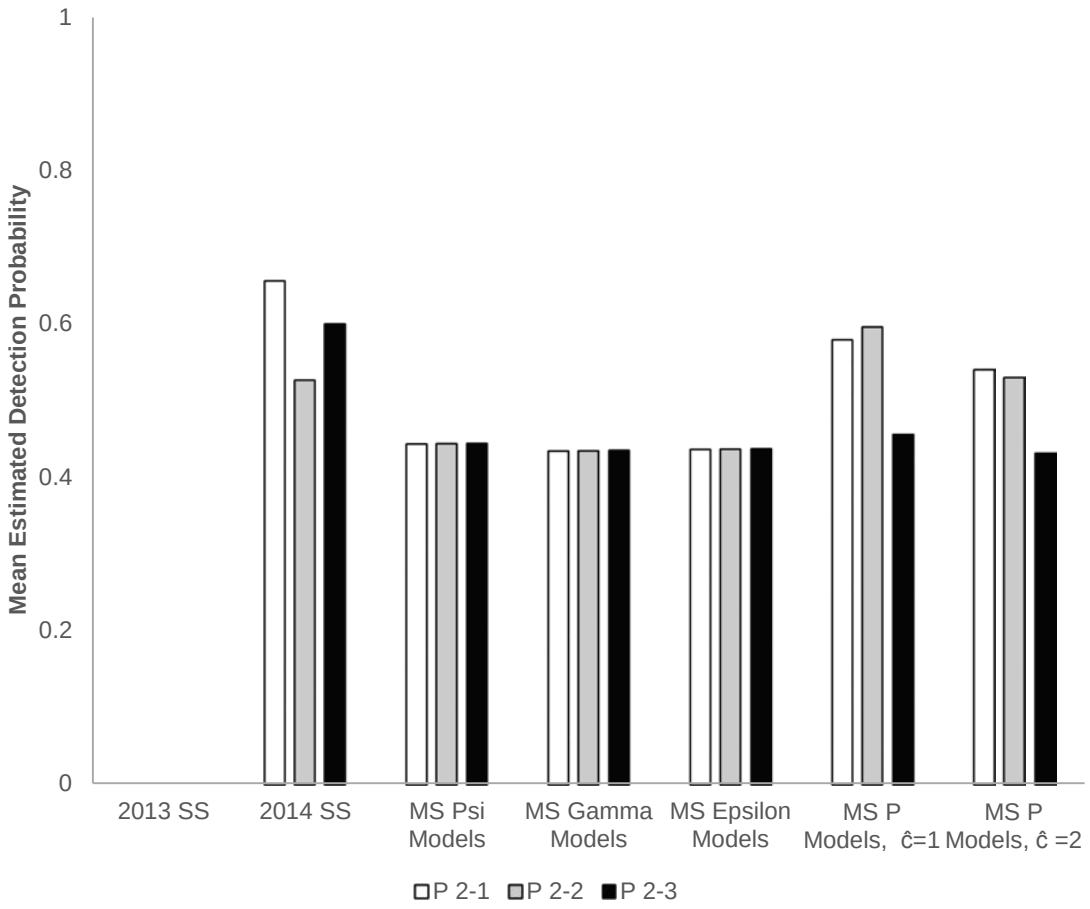

Figure 4. Model-averaged estimates of copperbelly detection probability for 2014 from single-season and multiple-season models.

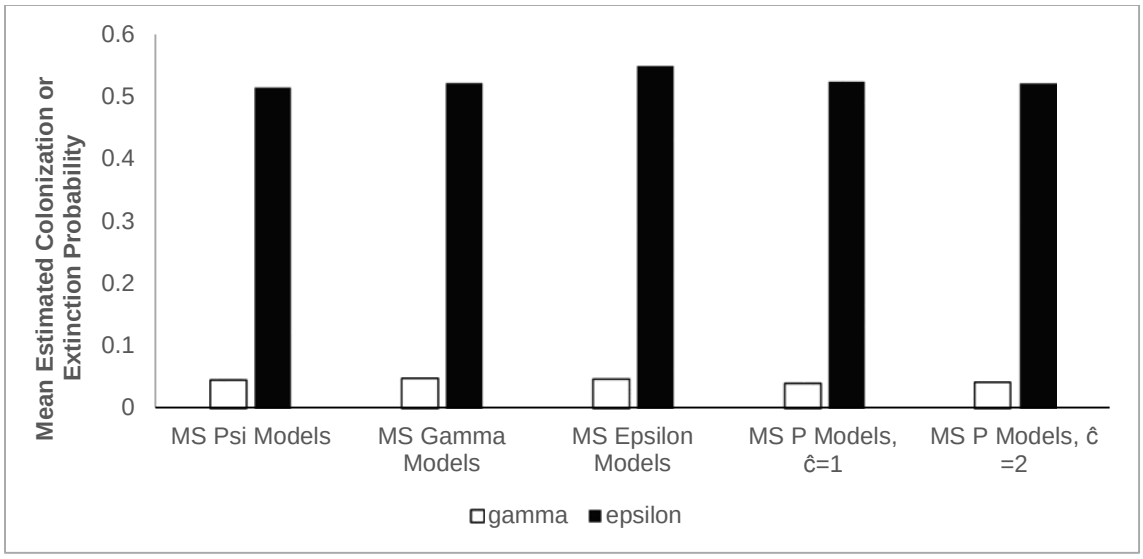

Figure 5. Model-averaged estimates of copperbelly colonization and extinction probabilities between 2013 and 2014 from single-season and multiple-season models.

Royle N-Mixture Models for Copperbellies and Northerns

Models for the two species indicated low abundance and densities of copperbellies at my study site, especially compared to northerns which had abundance and density estimates 4 or more times higher than copperbellies.

For both copperbellies and northerns, the top-ranked model for the Royle N-Mixture candidate sets was based on a negative binomial prior distribution (Tables 28 – 31). Since I did not use covariates to model heterogeneity in sites to avoid overparameterization in this model, my data are likely to be overdispersed compared to a Poisson distribution making the negative binomial a better choice for model to begin with (Royle, 2004, Royle *et al.*, 2005).

In both 2013 and 2014, northerns had much larger estimates of abundance per wetland site and overall abundance at my whole study area

(Table 32). Density of northerns was about 4 to 6 times that of copperbellies, and overall northern watersnake abundance was approximately 4 to 7.5 times that of copperbellies. This is not surprising given that there were 51 northerns observed in 2013 and 48 in 2014, compared to 12 copperbellies in 2013 and 14 in 2014. The much larger abundance and density of northerns than copperbellies is also supported by previous studies in the area (Lee *et al*., 2007). In 2012 and 2013, they observed 4-5 times as many northerns as copperbellies.

Violation of Closure Assumption

One of the assumptions of occupancy modeling is that sites remain closed to changes in occupancy status within seasons. In other words, a site is either occupied or unoccupied for a whole season, with no local extinctions or colonizations occurring. Based on telemetry studies of copperbelly movement patterns (for example, Roe *et al.*, 2003 and Herbert, 2003), this assumption is likely to be violated for copperbellies in this study due to their vagility within the timescales in which I completed surveying. In simulation studies, Rota *et al.* (2009) found that when the closure assumption is violated, models will tend to overestimate ψ. Bias will be more pronounced in models with constant detection probability than models with survey-specific detection probability, as changing detection probabilities absorbs some of the effect of movement (Mackenzie *et al*., 2006).

In order to relax the closure assumption, Kendall *et al*. (2013) developed staggered-entry or -departure models that permit one delayed arrival and/or one

early departure of a species at each site. I did not use these models for two reasons: first, these models are most suited to species whose biology makes it likely that they will be at a site for only a certain length of time (such as amphibians arriving at a pond and staying until breeding season is over), whereas copperbellies come and go from wetlands frequently, and second, these models introduce more parameters than basic occupancy models, and with such a small sample size in my study my models are already at risk of overparameterization.

In the future the issue of violation of the closure assumption could be dealt with by shortening survey windows to timescales at which copperbellies are likely to remain at one wetland (a matter of days), although as was the case with this study, logistical and personnel constraints may make this unrealistic if similar shoreline transect methods are employed. I attempted an alternative method (camera traps and basking platforms) with little success for copperbellies, although other herpetofaunal species were often observed. In the future, I suggest exploring the use of minnow traps checked daily at a large number of sites as an alternative. If survey length was short (several days), violation of the closure assumption is less likely. This method was employed by Durso *et al*. (2011) for an occupancy study of seven species of aquatic snakes including two *Nerodia*, *N. fasciata* and *N. floridana*.

Another way of dealing with the closure assumption violation for copperbellies would be to use larger sites so that it is unlikely that changes in occupancy status of a site would occur within a season. It may be realistic to

assume that copperbellies stay at one wetland complex throughout a season, although to get a large enough sampling size for occupancy modeling using wetland complexes as sites would require substantially more effort and time than was possible in this study.

In my study, I followed the lead of previous studies of copperbelly occupancy (Monfils & Lee, 2011, Lee *et al.*, 2011, and Lee & Kingsbury, 2014) and used wetlands instead of complexes as sites. Because closure assumptions are likely to be violated, ψ should be viewed as proportion of wetlands used by copperbellies rather than proportion of sites occupied and p should be viewed as the probability that the species is present and detected at the time of surveying rather than the probability of detecting the species if it is present. These estimates can be used as long as movement in and out of sites is random; otherwise, bias in ψ and p can be expected, as discussed above (Kendall *et al*., 2013, Lee *et al*., 2011).

Description of Sites Occupied by Copperbellies

I observed copperbellies at 7 wetlands during the course of this study (2013-2014). The wetlands at which copperbellies were found were all located toward the center of the area containing the sites in this study. These wetlands are all located within 1.5 kilometers of each other. For reference, the two farthest wetland sites included in the study are ~6 kilometers away from each other. Based on the spatial distribution of the copperbellies observed in this study and the movement patterns described by the telemetry studies of Roe *et al*. (2004), I

believe these copperbellies are part of a single metapopulation whose range does not extend throughout the whole study site. At the 7 “occupied” wetlands, copperbellies were often observed during multiple surveys and sometimes during both years. I believe most of these wetlands are “hotspots” for copperbelly activity in the area of the metapopulation, and that although copperbellies do move between wetlands frequently, they exhibit some site fidelity toward “favorite” wetlands and specific areas of shoreline. This belief was also expressed in Lee *et al.* (2011). Table 33 provides a summary of habitat characteristics of the “occupied” wetlands from my study.

The seven wetlands had varying border lengths (in meters): 85, 160, 344, 500, 962, 995, and 2245. For reference, the average wetland border length in this study was ~328 meters. Out of all wetland sites surveyed, the 3 wetlands with the largest border lengths had copperbelly observations, and were between 1.75 and 5 standard deviations above the mean wetland border length. These wetlands were also permanent, although 3 smaller wetlands that had copperbelly observations were ephemeral. Accordingly, the copperbelly observations at the ephemeral wetlands were earlier in the season (never in window 3) but that was not the case for the permanent wetlands. As mentioned previously, it makes sense that as wetlands dry up, copperbellies move to more permanent bodies of water with anuran prey still available. Of the 56 study sites, 31 were ephemeral and 25 were permanent based on presence or absence of water in autumn.

Of the 7 “occupied” wetlands, 3 were classified as palustrine open water (POW), 2 were classified as palustrine forested wetland (PFW), and 2 were

classified as palustrine shrub-scrub (PSS). I classified the wetlands in late summer and early autumn when vegetation was fully leafed out. The POWs contained water year-round. By definition, POWs have little total canopy cover (1%, 3%, and 10% in this case) or emergent vegetation (1%, 1%, and 15% in this case). The PFWs had more total canopy cover (90% and 95%) and emergent vegetation (30% and 20%) than the POWS. The PSSs also had more total canopy cover (65% and 55%) and emergent vegetation (64% and 95%) than the POWs. Because wetland classification is based on canopy and emergent vegetation cover, wetlands can be classified as different types at different times. In particular, there would be a much higher proportion of POWs earlier in the season, which would turn into other wetland types as vegetation leafed out. Copperbellies were only observed at POWs toward the end of the season, but were present early in the season at the wetlands later classified as PFWs and PSSs, when these wetlands would have been classified as POWs. Based on the observations in this study, copperbellies seem to prefer wetlands that have little canopy or emergent vegetation cover. This finding is supported by other sources (Hyslop, 2001, Herbert, 2003), which showed negative correlations between canopy cover and copperbelly use.

Of the 7 wetlands with copperbelly observations, 5 of 7 (71.4%) contained buttonbush and 1 of 7 (14.3%) contained dead ash trees. Within the study area, both species were relatively common at wetland sites. Of the 56 study sites, 30 contained buttonbush (53.6%) and 32 contained dead ash (57.1%).

I determined the percentage of each wetland's shoreline for various microhabitat cover types (cattail, herbaceous, shrub, woody debris, ground, and tree). For all study wetlands, herbaceous vegetation had the highest average percentage (30%), followed by woody debris (22%), shrubs (20%), and bare ground (19%). Cattails and trees both had small average percentages for all wetlands (3% and 5% respectively). For the 7 "occupied" wetlands, shoreline percentages of cattail, herbaceous cover, and trees were all within one standard deviation of the sample means. Four of the 7 wetlands (the 3 POWs and 1 of the PSSs) had shoreline shrub cover percentages more than 1 standard deviation from the sample mean. Shrub cover made up 46 – 69% of the shorelines of these wetlands. Given that these numbers are much higher than the average of all wetlands (20%), a number which includes many PSSs that might be expected to have more shrub cover than open water wetlands, shoreline shrub cover may be an important factor for copperbellies. This inference is supported by the findings of Herbert (2003), who suggested copperbellies prefer habitats with abundant shrub cover and herbaceous cover. The 2 PFWs with copperbelly observations had shoreline percentages of bare ground more than 2.5 standard deviations from the sample mean's average, although biologically this makes sense. Palustrine forested wetlands tend to have complete or near complete canopy cover, which would hinder growth of herbaceous or shrubby vegetation on the shoreline compared to wetland types with more open canopies (such as POWs or PEM/SEDGEs). It is somewhat unexpected that copperbellies were observed at these two PFWs, given the large amount of bare ground on the

shoreline and the nearly complete canopy closure (90% and 95% by the end of the summer). However, copperbellies were observed at the PFWs prior to full canopy closure, and both wetlands had more than 20% of the shoreline composed of other cover types (shrub or woody) which may be adequate for protection from predators. Five of the 7 “occupied” wetlands had woody debris shoreline cover percentages at or near zero, more than one standard deviation below the sample mean. The beta parameters from the top-ranked 2014 single-season copperbelly models (Table 11) indicated a negative correlation between amount of woody debris on the shoreline and copperbelly presence using this same habitat covariate dataset. As I previously mentioned, woody debris on the shoreline is negatively correlated with other cover types such as herbaceous and shrubby cover, which may be more preferable to copperbellies. Herbert (2003) found that copperbellies prefer habitats with stratified herbaceous and shrub cover, which supports this inference. However, he and Lee *et al*. (2007) also found copperbellies perched on logs or other woody debris often, indicating that copperbellies will use woody debris if it is present.

I classified macrohabitat amounts around wetlands and evaluated the four main types observed (forest, shrub-scrub, herbaceous or field, and roads with low traffic or foot traffic). Around the whole sample of wetlands surveyed forest was the dominant macrohabitat type (56% of macrohabitat observed), followed by herbaceous cover or fields (20%), shrub-scrub (15%), and roads with low traffic volumes or foot traffic (7%). Other macrohabitat types not covered by these 4 categories made up less than 2% of macrohabitat observed. Five of the 7

wetlands at which copperbellies were observed had over 50% forest (50% - 90%) surrounding them, which is not surprising because forest was the dominant macrohabitat type around all study sites. The first wetland also had over 40% low traffic or foot traffic roads in the surrounding macrohabitat in addition to forest. This wetland is surrounded by outdoor recreational activities and people throughout the summer, although copperbellies are still frequently observed there. Low traffic roads made up a smaller proportion of macrohabitat (<10%) for all other “occupied” wetlands, but 6 of the 7 wetlands had at least one low traffic or foot traffic road within 20 meters of the shoreline. During the copperbelly active season these roads have low to high volumes of foot traffic, lawnmowers or ATVs, and occasionally cars. Out of the sample of 56 surveyed wetlands, 23 (41%) do not have any roads (low, medium, nor high traffic volumes) within 20 meters of the shoreline. It is possible that low traffic or foot traffic roads have only minor or no impacts on copperbelly presence, or that roads didn’t make up a substantial enough proportion of the macrohabitat at these sites to greatly influence copperbelly presence. Furthermore, heavier traffic volumes might have greater impacts on copperbelly occupancy: only 1 of 7 “occupied” wetlands was within 20 meters of a medium traffic road (unpaved county road) and no “occupied” wetlands were within 20 meters of the high traffic roads in the area. Mortality risk from vehicles would be lower on roads with few vehicles and slower speed limits than on paved roads which get used much more frequently and at higher speeds. These inferences about copperbellies and proximity to roads are supported by Attum *et al*. (2008) who found that copperbellies are more likely to

occupy wetlands farther from roads than their more common congener, northerns. The last two macrohabitat types, herbaceous/field and shrub-scrub, had values for the 7 “occupied” wetlands that all fell within one standard deviation of the sample mean. All but 1 of these wetlands had at least some herbaceous or shrubby macrohabitat within 20 meters of the shoreline with the exception of a small PFW surrounded by only forest (94%) and a small footpath that occasionally had bicycles or ATVs (6%). Forest and absence of roads seem to be more important macrohabitat features than herbaceous or shrubby cover, based on these data.

In this study, copperbellies were observed at multiple wetland types with differing hydroperiods, border lengths, canopy cover amounts, emergent vegetation amounts, shoreline cover types, and macrohabitat types. However, by evaluating the habitat characteristics of wetlands at which copperbellies were observed and comparing them to habitat characteristics of the whole sample of wetlands, a few possibly important variables emerged. The three wetlands with the longest border lengths of the whole sample had copperbellies present, and 5 of the 7 “occupied” sites had border lengths longer than the sample average, which may indicate an association between wetland border length and copperbelly use. Observations of copperbellies appeared to be correlated with POW-type wetlands with little or no canopy cover nor emergent vegetation, whether at the beginning of the active season before vegetation leafed out, or later in the year at wetlands that remained POWs year-round. Shoreline shrub cover was present at copperbelly-“occupied” wetlands more than might be

expected based on the average shoreline shrub cover from the whole sample of wetlands. The “occupied” wetlands also tended to have lower than average woody debris shoreline cover, which could be indicative of a negative correlation between copperbelly use and woody debris cover. Additionally, these wetlands tended to have large proportions of forest macrohabitat within 20 meters of the shoreline, although the average amount for all study sites was over 50% already. Even if forested macrohabitat influences copperbelly wetland preference, it is abundant throughout the study site and therefore likely not a limiting factor on copperbelly wetland choice. Lastly, roads were not uncommon within 20 meters of the shoreline of “occupied” wetlands. However, these roads had only low or foot traffic (with the exception of one unpaved county road). No “occupied” wetlands had heavily trafficked roads within 20m of the shoreline, which could be indicative of avoidance of roads or lower mortality rates away from heavily trafficked roads.

Table 33. Characteristics of wetlands occupied by copperbellies compared to characteristics of all wetlands in the study sample. For continuous variables, the average of values for all study wetlands is listed and the range of values is given in parentheses.

	W1	W2	W3	W4	W5	W6	W7	All Study Wetlands
# times observed per total amount surveys	3 of 6	2 of 6	4 of 6	2 of 6	1 of 6	1 of 6	1 of 5	14 of 299
Border length (m)	995	500	2245	160	344	962	85	328 (63 – 2245)
Contains water?	Yes	No	Yes	No	Yes	Yes	No	25 Yes 31 No
Wetland type	POW	PFW	POW	PFW	POW	PSS	PSS	15 PFW 23 POW 13 PSS 5 PEM/SEDGE
Total canopy cover	1%	90%	3%	95%	10%	65%	55%	44.5% (0 – 100%)
Tree canopy cover	1%	65%	1%	75%	0%	5%	5%	23.25% (0 – 90%)
Subcanopy cover	1%	10%	1%	10%	0%	12%	0%	7.3% (0 – 45%)
Shrub canopy cover	0%	25%	1%	20%	10%	62%	50%	25.41% (0 – 100%)
Emergent vegetation	1%	30%	1%	20%	15%	64%	95%	38.36% (0 – 100%)
Buttonbush present?	Yes	Yes	No	Yes	Yes	Yes	No	30 Yes 26 No
Dead ash present?	No	No	No	No	No	Yes	No	32 Yes 24 No
Shoreline cattail	8%	0%	1%	0%	1%	0%	0%	3% (0 – 41%)
Shoreline herbaceous	27%	0%	25%	0%	27%	5%	35%	30% (0 – 100%)

Table 33, continued.

Shoreline shrub	46%	4%	51%	23%	69%	26%	62%	20% (0 – 98%)
Shoreline woody	6%	16%	2%	0%	3%	29%	2%	22% (0 – 55%)
Shoreline ground	6%	74%	6%	77%	0%	35%	0%	19% (0 – 77%)
Shoreline tree	1%	5%	10%	0%	0%	5%	0%	5% (0 – 19%)
Macrohabitat forest	50%	80%	53%	94%	9%	79%	13%	56% (0 – 100%)
Macrohabitat shrub-scrub	8%	0%	22%	0%	16%	10%	50%	15% (0 – 81%)
Macrohabitat herbaceous/ field	0%	18%	14%	0%	69%	2%	25%	20% (0 – 100%)
Macrohabitat roads (low/ foot traffic)	42%	0%	8%	6%	6%	10%	6%	7% (0 – 50%)

Management Recommendations

Many recent studies have reported the dire status of the Northern population segment of copperbellies. Lee *et al.* (2007) and Attum *et al.* (2009) estimated very low abundance and density rates of copperbellies in the area. Lee & Kingsbury (2014) reported high extinction rates, low colonization probabilities, low abundance and density estimates, and lower occupancy than northerns in the area. My study had similar findings to Lee & Kingsbury (2014): low abundance estimates for copperbellies in my study area, as well as low density at wetland sites, high extinction probabilities, and low colonization probabilities.

Because of the dire status of the NPS of copperbellies, my first recommendation is to upgrade the federal status of this population to endangered. I agree with the statement by Attum *et al*. (2009) that copperbellies are already endangered. The federal copperbelly recovery plan lists the criteria for reclassifying copperbellies as either of the following: no metapopulations of 500+ adults or total population size less than 1000 individuals (USFWS, 2008). Given the extremely low abundance estimates of my study and previous studies, I believe reclassification as endangered is long overdue.

My second recommendation is that habitat in the area of the NPS of copperbellies be protected or restored. Especially important are wetlands with large border lengths, little or no canopy cover nor emergent vegetation, and stratified shoreline cover.

My last recommendation is to implement a juvenile headstarting program for copperbellies to supplement the natural population. Roe *et al*. (2015) recently reported success with this technique using northerns. Their study provides a foundation for the use of this technique with copperbellies.

CONCLUSION

I used occupancy modeling in Program PRESENCE to estimate various population parameters for the imperiled Northern population segment of copperbellies, including site occupancy, detection probabilities, site colonization and extinction rates, and abundance and density. I also compared these estimates to those of the Northern Watersnake. Through occupancy modeling I was able to discover a few covariate relationships with population parameters for copperbellies. Furthermore, I gave detailed natural history descriptions of sites occupied by copperbellies and discovered some habitat features common to these wetlands, some of which were supported by the modeling analyses and all of which may warrant additional exploration.

For both copperbellies and northerns, possible covariate relationships with population parameters were elucidated. The most supported result of modeling was that wetland border length consistently had a positive relationship with snake occupancy. Large wetlands appear to be very important for both species. Several models also showed negative relationships between detection probabilities and progression of the survey season, which has implications for future study designs.

Estimates of population parameters from this study supported what was already known from previous studies such as Lee & Kingsbury (2014): copperbellies are rare in the area, have low site-occupancy, and have low overall abundance and density, especially when compared to northerns. They also have high extinction probabilities and low colonization probabilities, which makes the future of this already small and declining population even more dire.

Low overall sample size may have been an issue for modeling for both copperbellies and northerns, although the effect was worse with copperbellies because there were also few detections. With small sample sizes and few detections, models often fail to converge and have dispersion issues. Furthermore, it is not appropriate to fit models with many parameters to sparse data, so elucidating covariate relationships with population parameters is difficult in these situations. With vagile species such as copperbellies, model assumptions are likely to be violated as well.

Because of these problems, I recommended that future studies look for alternatives to occupancy modeling unless methods are changed (one possibility I have previously mentioned is using minnow traps instead of visual encounter surveys). I believe *much* more intense sampling effort (sampling more sites in a shorter amount of time) is required if shoreline surveying for the purpose of occupancy modeling is to be used in our ongoing efforts to monitor this population.

I recommended future efforts should attempt to estimate population size for the Northern population segment of copperbellies. Based on the already dire

status of copperbellies in the area (low abundance, high extinction probabilities), I also recommended that the federal status of this population segment should be reevaluated.

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LITERATURE CITED

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APPENDIX

APPENDIX

Table A1. Pearson's product-moment correlation p-values for site-specific covariates. Bold values highlight significant values (α = 0.00017). Significance level was adjusted to correct for false discovery using the Benjamini-Hochberg procedure with a false discovery rate of 0.001. Number of correlations for each covariate includes correlations from rows and columns with the covariate name.

	road m/h traffic	road low traffic	macro herb./field	macro shrub-scrub	macro forest	shore tree
contains water	0.8214	0.0019	0.1064	**5.54E-05**	**8.26E-06**	0.0027
avg. aquatic veg.	0.0667	0.7547	0.0384	0.0514	0.0094	0.0005
avg. woody abund.	0.0007	0.0717	0.0161	0.0312	**1.28E-04**	0.0002
dead ash	0.4607	0.0052	0.1732	0.5578	0.0350	0.1431
buttonbush	0.1236	0.0123	0.1083	0.0049	0.0002	0.1968
total canopy cover	0.5109	0.0017	0.0039	0.0002	**6.00E-08**	**1.24E-05**
tree canopy cover	0.5737	0.0833	0.0427	**1.22E-04**	**6.25E-05**	**7.32E-05**
subcanopy cover	0.8854	0.0632	0.0746	0.0049	0.0008	0.0014
shrub canopy cover	0.5406	0.0042	0.0300	0.0827	0.0004	0.0156
% emergent veg.	0.0345	0.0015	0.8681	0.2321	0.1901	0.5445
POW	0.1976	0.0018	0.1505	0.0054	0.0006	0.0050
PSS	0.9953	0.0422	0.1240	0.6878	0.0352	0.2907
PFW	0.6781	0.1532	0.1413	0.0016	0.0022	0.0010
PEM/SEDGE	0.0029	0.9977	0.9977	0.5152	0.0404	0.0731
total border	0.6404	0.1376	0.8280	0.9586	0.4430	0.7765
shore cattail	0.1227	0.6749	0.0149	0.5929	0.0554	0.0354
shore herbaceous	0.0067	0.9982	**1.91E-06**	0.1828	**7.30E-06**	**3.50E-06**
shore shrub	0.9463	0.0021	0.6738	0.0008	0.0271	0.0252
shore wood	0.0191	0.0305	0.0041	0.0753	**4.37E-05**	**8.62E-05**
shore ground	0.0537	0.0388	0.0004	**1.03E-04**	**0**	**6.00E-08**
shore tree	0.0414	0.0299	0.0004	0.0091	**2.20E-07**	
macro forest	0.0452	0.0216	**0**	**3.50E-07**		
macro shrub-scrub	0.2695	0.0432	0.8480			
macro herb./field	0.3820	0.6067				
road low traffic	0.6067					
# of correlations	*0*	*0*	*2*	*4*	*10*	*6*

Table A1, continued.

	shore ground	shore wood	shore shrub	shore herbaceous	shore cattail	total border
contains water	**1.18E-06**	0.0349	0.0136	0.0553	0.0092	0.0006
avg. aquatic veg.	**1.32E-05**	0.0173	0.0171	0.0083	0.4683	0.6759
avg. woody abund.	**6.68E-05**	**0**	0.1641	**1.70E-06**	0.0583	0.1756
dead ash	0.1431	**3.60E-06**	0.0146	0.1251	0.7298	0.9202
buttonbush	0.0009	0.1166	0.6315	0.0036	0.8900	0.9242
total canopy cover	**0**	0.0009	0.1583	**1.73E-06**	0.0252	0.0967
tree canopy cover	**0**	0.0016	0.0062	0.0004	0.1341	0.1667
subcanopy cover	0.0061	0.0010	0.0758	0.0228	0.2240	0.6462
shrub canopy cover	0.0048	0.0961	0.5868	0.0008	0.0757	0.3314
% emergent veg.	0.4108	1.0000	0.7939	0.9057	0.3884	0.1205
POW	**5.31E-05**	0.0288	0.0987	0.0281	0.0137	0.0237
PSS	0.5133	0.3728	0.2385	0.0829	0.1690	0.4368
PFW	**8.00E-08**	0.0057	0.0083	0.0029	0.3038	0.3606
PEM/SEDGE	0.0635	0.0723	0.5623	0.0006	0.5980	0.2087
total border	0.1761	0.2503	0.3852	0.8406	0.0867	
shore cattail	0.0758	0.1317	0.2870	0.1671		
shore herbaceous	**6.00E-08**	0.0020	0.0311			
shore shrub	0.0055	0.0003				
shore wood	0.0046					
shore ground						
shore tree						
macro forest						
macro shrub-scrub						
macro herb./field						
road low traffic						
# of correlations	*11*	*4*	*0*	*6*	*0*	*0*

Table A1, continued.

	PEM/SEDGE	PFW	PSS	POW	% emergent veg.	shrub canopy cover	subcanopy cover
contains water	0.2534	0.0003	0.0767	**0**	0.0009	0.0021	0.0012
avg. aquatic veg.	0.0184	**2.70E-07**	0.0013	0.8756	0.0002	0.0791	0.0493
avg. woody abund.	0.0019	0.0036	0.0393	0.0089	0.7630	0.0008	0.0032
dead ash	0.0813	0.1437	0.3237	0.2472	0.5465	0.0618	0.0141
buttonbush	0.1189	0.5677	0.0010	0.0182	0.0018	**5.30E-07**	0.0662
total canopy cover	0.0281	**1.00E-07**	0.0002	**0**	0.0006	**0**	**3.01E-06**
tree canopy cover	0.1366	**0**	0.2833	**1.68E-06**	0.9149	0.1909	**6.85E-06**
subcanopy cover	0.3780	**5.51E-06**	0.7469	0.0002	0.2286	0.0365	
shrub canopy cover	0.0785	0.6467	**0**	**2.24E-06**	**0**		
% emergent veg.	0.0016	0.4908	**6.30E-07**	**1.00E-08**			
POW	0.0517	**7.21E-05**	0.0004				
PSS	0.2047	0.0123					
PFW	0.1621						
PEM/SEDGE							
total border							
shore cattail							
shore herbaceous							
shore shrub							
shore wood							
shore ground							
shore tree							
macro forest							
macro shrub-scrub							
macro herb./field							
road low traffic							
# of correlations	*0*	*6*	*2*	*7*	*3*	*5*	*3*

Table A1, continued.

	tree canopy cover	total canopy cover	buttonbush	dead ash	avg. woody abund.	avg. aquatic veg.	contains water
contains water	**1.21E-06**	**3.00E-08**	0.0031	0.8796	0.0172	0.0561	
avg. aquatic veg.	**1.21E-06**	0.0759	0.9918	0.7139	0.0095		
avg. woody abund.	0.0003	**5.20E-07**	0.0066	0.0002			
dead ash	0.1229	0.0346	0.3234				
buttonbush	0.1229	**8.90E-05**					
total canopy cover	**0**						
tree canopy cover							
subcanopy cover							
shrub canopy cover							
% emergent veg.							
POW							
PSS							
PFW							
PEM/SEDGE							
total border							
shore cattail							
shore herbaceous							
shore shrub							
shore wood							
shore ground							
shore tree							
macro forest							
macro shrub-scrub							
macro herb./field							
road low traffic							
# of correlations	*10*	*12*	*2*	*1*	*5*	*3*	*6*